

## **A synopsis of the platyrhacid millipeds of Borneo (Diplopoda: Polydesmida: Platyrhacidae)<sup>1</sup>**

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**A synopsis of the platyrhacid millipeds of Borneo (Diplopoda: Polydesmida: Platyrhacidae).** - The 37 species of Platyrhacidae known to inhabit Borneo are surveyed in the context of a modern classification, with historical summary and discussion of taxonomic characters. Three tribes and eight genera are recognized: Platyrhacini with *Stenoniodes*, *Acanthodesmus*, *Eurydirorhachis*, and *Arbelorhacus* gen. n. (type *A. magirus*, sp. n.); Phyodesmini with *Phyodesmus* only; and Hoplurorhachini (trib. n.) with *Hoplurorhachis* (type *H. everetti* Pocock, also *H. oeceter* sp. n. and *H. crassipes* (Carl) comb. n., *Creagronopus* gen. n. (type *hosei* Pocock), and *Sabarhacus* gen. n. (type *S. derodontus* sp. n., also *sucidus* Attems). Keys to tribes, genera, and the species of some genera are provided.

**Key-words:** Diplopoda - Polydesmida - Platyrhacidae - Borneo.

### INTRODUCTION

During several expeditions to northern and western regions of Borneo in 1982, 1987 and 1988, Dr Bernd Hauser (former Curator, Department of Arthropods and Lower Insects, Geneva Natural History Museum, Switzerland) made particular efforts to obtain material of the soil and litter fauna of arthropods. Among the numerous forms of Diplopoda thus collected were several interesting species of the polydesmidan family Platyrhacidae which were entrusted to me for identification and possible report. This makes a suite of three preceeding studies (Mauriès, 1989; Hoffman, 1993; Golovatch, 1996).

Platyrhacid millipeds comprise a large and diverse group of arthropods with an interesting distribution. One faunule occupies the Neotropical region between Peru and Nicaragua, a second occurs in southeast Asia and the Greater Sunda islands, and the third is confined to the Philippine-Papuan archipelagos from Luzon and Sulawesi to the Solomons. The vast disjunction between Neotropical and Australasian components invites careful study and analysis of its history, as do the patterns of speciation in the south Pacific island chains. Platyrhacids are large, conspicuous and often colorful animals, they are well represented in museum collections, and should have attracted the devoted attention of many systematists.

<sup>1</sup> Diplopoda from Borneo in the Muséum d'histoire naturelle de Genève. 4.

Regrettably, this bounty of biogeographic potential has so far been only marginally investigated, thus sharing the common heritage of Diplopoda generally. Although the family is distinctly set off from other polydesmidans by rather clear characters, its internal classification has become increasingly more confused and unsatisfactory over the past century instead of achieving progressively greater maturity as one might expect from the analogy of most other groups of organisms.

Aside from the failure of any systematist to undertake a revision of the entire family, most of the problems afflicting the Platyrrhacidae, precluding any comprehension of its former distributional dynamics, can be attributed to the influence of Carl Attems and R. V. Chamberlin, the two specialists who contributed most to knowledge of the group after 1900.

Attems followed an extremely conservative taxonomic approach, and by all conventional criteria could only be considered as a "lumper". His interest in both millipeds and centipeds worldwide allowed scant time for deliberate, meditative evaluation of the species he described, he utilized "key character" diagnosis for both species and genera, ignored inconvenient rules of nomenclature, paid scant attention to biogeographic implications, and tended to recognize genera of awe-inspiring heterogeneity. Most of these mannerisms were not unusual for his time, however, and, to his credit, Attems made special efforts to provide useful keys and literature citations for the groups that he studied.

Chamberlin likewise worked with many kinds of organisms: millipeds, centipeds, and spiders, all on a world-wide basis, so that his time and energies were extended to a maximum. Perhaps as a result his major interest appears to have been the publication of new names with an absolute minimum of documentation or comparison with already known taxa: he was uncontestedly a radical "splitter". Most of his later work was simply naming and describing the contents of various collections which came to his hand; preparation of syntheses rarely played more than an occasional and very superficial role. Probably the majority of his new species could not be recognized from the original descriptions, even when illustrations were included, making examination of his types mandatory.

It can be appreciated from this prologue that the combined effects of an ultraconservative synthesis approach and one of irresponsible analysis brought the classification of the Platyrrhacidae into a condition of essential incomprehensibility by the middle of this century. Since that time, some efforts have been made at revision of selected genera using modern systematic principles, but the critical monographic treatment has not yet been undertaken. Until that effort has been made, studies either of isolated genera or regional faunas offer the only hope for amelioration.

Even the flawed state of current knowledge reveals that the greatest generic diversity of platyrrhacids occurs on the island of Borneo. Therefore, a clarification of that fauna is obviously crucial for any better understanding of relationships in the entire family. At various times in the past, it has been my good fortune to examine material which facilitated some elementary taxonomic and nomenclatorial studies of some Bornean genera (e.g., *Phyodesmus* in 1978, *Acanthodesmus* in 1984). Other major components have been studied to some extent also, but not accorded formal

treatment until the examination of Dr Hauser's Sabah collections afforded the necessary impetus and opportunity.

It will be immediately obvious that the present synoptic review is scarcely more than an annotated outline, yet it is presented with the conviction that natural generic groups, composed largely of species either poorly-known or rescued from the obscurity of placement in "*Platyrhacus*", are defined for possible later attention. The status of several species must here be passed over in virtual silence, for reasons to be accounted in a subsequent paragraph.

In addition to the material of the Geneva Natural History Museum [MHNG], I have examined some relevant types in The Natural History Museum, London [BMNH], the Natural History Museum, Vienna [NMW], the Natural History Museum, City of Genova (MCSNG) and the Museum of Comparative Zoology [MCZ], several specimens submitted for identification by Dr John Kethley of the Field Museum of Natural History [FMNH], and a few others in the Virginia Museum of Natural History, Martinsville [VMNH] from Sarawak kindly presented by Dr J. G. E. Lewis. The acronym SMF is used to designate the type depository of several species in the Senckenberg Museum, Frankfurt am Main.

#### Family **PLATYRHACIDAE** Pocock

*Platyrhachidae* Pocock, 1895: 788.

*Platyrhachidae* Attems, 1938: 202.

*Platyrhachidae* Hoffman, 1980: 162.

Diagnosis: A family of Chelodesmoidea characterized by the unmodified anterior legs and sterna in males, ozopores surrounded by broadened discoid peritremata, often at some distance from paranotal margin, apical broadening of the epiproct, and presence of "compound" setae on labrum (and often also on the epiproct). Prozonal texture finely to coarsely granulate. Stigmata, especially the anterior of each pair, distinctly enlarged and elevated. Tibiae of legs with distinctly enlarged, apparently socketed, dorso-apical macroseta. Vasa deferentia open flush on ventral surface of coxae of 2nd pair of legs. Gonopods typically simple in form, without prefemoral process. Gonosternal elements reduced or missing.

Components: 29 nominal genera are admitted to the family in the most recent list (Hoffman, 1980), to which total three additional genera are proposed in this paper.

Gonopod structure: The male genitalia of most platyrhacids are basically of very simple construction: the coxae lack apophyses, the prefemora lack processes in all but one or two species, and the telopodite usually terminates in a small slender solenomere and larger, shielding tibiotarsal element. This pattern is completely pervasive in the American fauna and dominant elsewhere, sometimes even the tibiotarsal element may be missing. However, in Borneo, the Lesser Sundas, and the Papuanian archipelago, the telopodite is frequently equipped with as many as four additional processes.

It is still unclear to me whether a lesser number represents secondary loss or an additive stage, on the way to five. If the derivation of polydesmidan gonopods from modified 7th legs is emphasized, then the simplest (most leg-like) gonopod would



seem ipso facto to be the generalized condition. A complex telopodite could then only be regarded as derivative. But the capricity of animal evolution almost guarantees that some "simple" gonopods represent an early stage in a transformation series, and some have resulted from secondary reductions. At the present time I cannot distinguish which is which. From a strictly pragmatic and functional standpoint, it is reasonable to defer concern over this point and deal simply with the situation as it occurs. Among the known extant fauna, the most complex gonopod occurs in the genus *Parazodesmus*, endemic in the Solomon Islands and New Britain. In my 1984 paper on *Acanthodesmus* I provided an account of this pattern, basically five similar telopodite processes, and mentioned some of the many permutations that could be derived from it. For ease of reference and the relevance to the Bornean fauna, I give now an expanded version of that discussion, the more so as it gives the basis for the nomenclature here employed as the major basis for generic differentiation.

Because of substantial random convergence in the apparent loss or retention of telopodite branches in the Platyrrhacidae, the identification of these processes and establishment of homologies is extremely difficult. The pioneering work of Attems, although an obvious step in the right direction, is now known to be inconsistent and unreliable. During the past two decades I have been able to study a large number of Indomalayan and Papuan platyrrhacids and have been able in consequence to develop a classification and terminology for the gonopod elements which appears to be satisfactory. Reference should be made to Figure 1, showing the telopodite of *Parazodesmus verrucosus* in dorsal aspect, in connection with the following description.

The maximum number of processes so far known to occur is five. The solenomere, which is always present as the termination of the telopodite, is indicated by the letter **a**. The other four may be variously suppressed or enlarged in many ways and a large number of combinations has been recognized. Process **b** is the distalmost process adjacent to **a** and usually parallel to it; process **c** is typically much smaller than either **a** or **b** and is placed near their point of juncture. Process **e** is usually also quite small, and is located near the midlength of the telopodite. Of these five, processes **b** and **d** are located on the **outer** side of the prostatic groove as the gonopod is viewed in dorsal aspect (Fig. 1), whereas **c** and **e** occur on the **inner** side.

It is possible to express the foregoing symbolism in the form of simple formulae which are useful in mapping the distribution of species groups or genera. If some processes are distinctly larger or smaller than the others, upper and lower case letters reflect this fact. When two or more processes are grouped onto a common stalk the appropriate letters can be enclosed in brackets. I give below the gonopod formulae for several genera by way of illustration:

*Parazodesmus*: A, B, c, D, E

*Psaphodesmus*: (a,b,c) D, E

*Ozorhacus*: a, d, e

*Hoplurorhachis*: a, C, d

*Acanthodesmus*: A, b, c

*Platyrrhacus*: A, D

*Derodesmus*: a



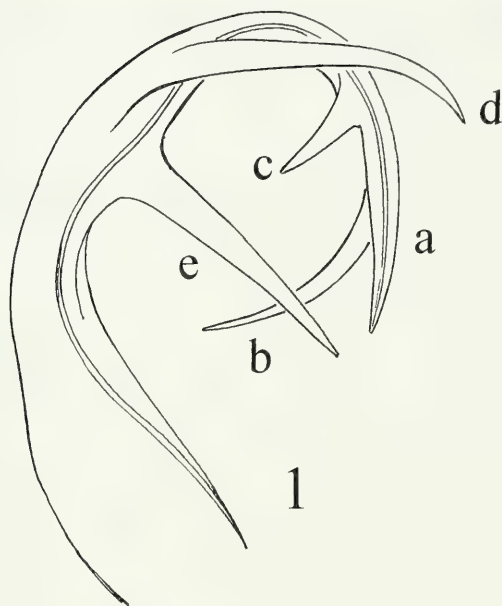


FIG. 1

*Parazodesmus verrucosus* (Pocock), left gonopod, dorsal aspect, showing basic psaphodesmine pattern of five telopodite processes from which all others can be derived by loss or shape modifications. Identification of structures by letters discussed in text.

As the addition, loss, or modification of individual gonopod parts is obviously liable to random expression, a certain amount of flexibility in the application of generic definitions is desirable. Thus some platyrhacid genera may be expected to contain species which do not conform to a formal diagnosis in every respect, but which are manifestly close relatives to most of the typical included taxa.

#### CLASSIFICATION OF BORNEAN PLATYRHACIDS

The first platyrhacids described from Borneo were five species collected mostly in the southern part by the malacologist E. von Martens and named by W. C. H. Peters in 1864. The next period of activity came in the 1890s, with the description of various new species by Silvestri (1896, 1899), Attems (1897), Cook (1896), and Pocock (1897). The last two in particular contributed most of our knowledge of this faunule, setting up new local genera as well as species. By 1914, Attems could list 26 species of Bornean platyrhacids; regrettably he discarded all of the available generic categories and lumped all species in his "Platyrhacus".

Subsequent to 1914, a few species were added by Chamberlin (1921) and Attems (1932). In 1938, Attems slightly liberalized his rigid generic concept, and recognized several of the older names in the status of subgenera. Since then, essen-

tially nothing was added to our knowledge of Borneo species until my short revisions of *Phyodesmus* (1978) and *Acanthodesmus* (1984) appeared. A full century after the promising early work by Pocock and Cook, the time for an overview of Borneo platyrhacids is long overdue, and thanks to the catalytic effect of Dr Hauser's collections, can now be attempted.

In terms of general relationships, some groupings are evident and may be examined briefly. Cook's pioneering survey of the Indomalayan fauna (1896) recognized 126 genera, some of which were based on specimens he personally studied in the Berlin museum and others on published descriptions, and several which had been proposed by Pocock, Peters, or Silvestri.

Regrettably, some of the Cook genera were based on genitalic characters, others on peripheral body form, so it was impossible to evaluate or compare these taxa consistently. Nonetheless, he went so far as to propose an intuitive suprageneric classification which proposed four subfamilies populated, in Cook's words, as follows (in 1896, Cook used the ending "-ini" instead of "-inae" which he later adopted):

"The *Phyodesmini* and *Taphodesmini* include as yet but a single genus each... To the *Psaphodesmini* may be referred *Derodesmus* and *Zodesmus*, while the remaining Malayan genera can be provisionally included in the *Acanthodesmini*, from which the separation of other subfamilies will doubtless be found convenient."

In the light of an additional century of investigation and a vast increase in the number of known taxa, Cook's inferences seem remarkably prescient. Although subfamily rank is probably too exalted, prior to a revision of the entire family, there seems to be justification for adopting the Cook categories at the level of tribe to imply magnitudes of similarity and differences.

Within the Borneo fauna, *Phyodesmus* is obviously disjunct, without apparent relatives there or elsewhere. The three taxa *Hoplurorhachis*, *Creagronopus*, and *Sabarhacus* comprise a cohesive endemic group (tribe). *Acanthodesmus*, *Eurydirorhachis*, *Stenoniodes*, and *Arbelorhacus* are provisionally combined into a tribe with *Platyrhacus* of the Java-Sumatra-Malaya region. The first two named are together somewhat disjunct and may later be extracted into a discrete tribe.

The tribal groupings of the Borneo genera are summarized in the following outline:

Phyodesmini Cook

*Phyodesmus* Cook, 1896 (revised by Hoffman, 1978)

Platyrhacini Pocock

*Acanthodesmus* Peters, 1865 (revised by Hoffman, 1984)

*Eurydirorhachis* Pocock, 1897 (revised by Hoffman, 1984)

*Stenoniodes* Pocock, 1897 (treated in this paper)

*Arbelorhacus* new genus

Hoplurorhachini new tribe

*Hoplurorhachis* Pocock, 1897 (treated in this paper)

*Sabarhacus* new genus

*Creagronopus* new genus

It may be emphasized that some of the foregoing names may be later shown to be synonymous with others proposed a year earlier (Cook, 1896) for species in the Indomalayan fauna.

Species of uncertain generic and tribal position

The enigmatic species described as *Platyrrhacus doryphorus* by Attems in 1899 cannot be placed anywhere with confidence in light of present knowledge, as the gonopod was only briefly described and no illustration was provided. Although the type specimen was said to be in the Berlin museum, I could find no trace of it there during four visits, and it was not documented by Moritz & Fischer (1978). Nor have searches in the collection at Vienna been any more successful. Unless the specimen or a gonopod preparation are located by serendipity, or topotypic material is obtained at Sintang, Borneo, the status of *doryphorus* will remain a mystery. Attems described the gonopod as follows. "... von der wie gewöhnlichen birnförmig angeschwollenen Basis des Schenkels ein schlanker, spitzer, langer Dorn entspringt. Der Schenkel setzt sich in einem einfachen, eingekrümmten, allmählich sich verjüngenden Endhaken ohne Verzweigung oder Seitenhaken fort." This description calls to mind an apparently similar structure that characterizes *Acanthodesmus anambasius* (cf. Fig. 37). Attems referred the species to his nominal subgenus *Haplorhacus*, but that taxon, as defined by the "simple" telopodite, is manifestly polyphyletic and it is unknown whether *doryphorus* is cladistically congeneric with *Haplorhacus haplopus*, the type species.

Lastly, a species described by Attems (1897) as *Platyrrhacus amauros* from "Batjan - Borneo - Ternate" from female specimens remains unknown to me, and resolution of its status may require some kind of arbitrary intervention. It is unlikely that such a species occurs both on Borneo and Ternate; mislabeling seems likely.

KEY TO THE BORNEO TRIBES OF *PLATYRHACIDAE*

1. Telopodite of gonopod (Fig. 23) nearly straight, occasionally slightly sinuous as seen in mesal aspect, the long prefemoral region apparently with a distal ensiform process on dorsal side (absent only in *P. longispinosus*); paranota large and almost horizontal, widest across anterior corners, lateral edge deeply incised and dentate (Fig. 22); dorsum brightly colored with blue, yellow, and black markings; very large species, adults more than 90 mm long. . . . . **Phyodesmini** Cook
- Telopodite of gonopod curved or bent dorsad over coxa, rarely (one exception) with trace of prefemoral process; paranota variable but never dentate laterally; dorsum without bright color patterns; adults less than 90 mm long . . . . . 2
2. Epiproct apically broadened with posterolateral corners acutely projecting, acute median projection often present (Fig. 6); paranota nearly rectangular in profile, anterior edge strigilate (Fig. 5). **Hoplurorhachini**, trib. n.
- Epiproct otherwise shaped; paranota variable but without strigilate anterior edge . . . . . **Platyrrhacini** Pocock



### Hoplurorhachini new tribe

Component: *Hoplurorhachis* Pocock, 1897, *Creagronopus* new genus, *Sabarhacus* new genus.

Diagnosis: Body form generally parallel-sided over segments 4-16; collum small, widest anteriorly; paranota of segments 2-4 small; those of midbody segments large, subhorizontal, appearing nearly square, with anterior edges strigilate, lateral smooth and straight, and posterior crenulate. Ozopores large, located near center of paranotal length, removed from lateral edge by varying distances. Metazona convex, faintly coriarius, posterior row of tubercles developed on most segments, anterior two rows evanescent. Epiproct with prominent caudolateral angles (Fig. 6). Sterna with four long acute subcoxal spines, directed ventrad or slightly caudad.

Gonopods large, coxae with setiform or penicillate dorsal hairs; prefemoral region of telopodite elongated, nearly straight; acropodite region recurved mesad. Process **e** of telopodite consistently absent, **c** always present.

#### KEY TO GENERA OF HOPLURORHACHINI

1. Process **d** of gonopod reduced, smaller than **a** (Fig. 8); gonocoxa without paracannular setae; ozopores removed from lateral edge of paranota by about 4X diameter of a peritreme (Fig. 5) . . . . . *Hoplurorhachis*
- Process **d** of gonopod enlarged, longer than main termination of telopodite (Fig. 10); gonocoxa with field of setae subtending base of cannula; ozopores removed from lateral edge of paranota by about 1 or 2X diameter of a peritreme (Fig. 13) . . . . . 2
2. Prefemoral region of telopodite unusually long, becoming broadest distally at point of curvature; process **d** very large, falciform, prolonged distad and curved beyond end of main termination, processes **a**, **b**, and **c** grouped at end of common stem (Figs 10, 11). . . . . *Creagronopus*
- Prefemoral region of telopodite tapering gradually distad and much shorter relative to total length of gonopod, third distal only gradually curved mesad, not bent at 90° angle; process **d** large and laminate, but not recurved falciform and but slightly longer than main termination, process **b** absent, **a** and **c** widely separated (Fig. 19) even though on a common stem . . . . . *Sabarhacus*

#### *Hoplurorhachis*

*Hoplurorhachis* Pocock, 1897: 437. Described with two new species. Type species: *H. everettii* Pocock, by original designation.

*Hoplurorhachis*: Hoffman 1980: 163.

Diagnosis: Gonopod coxa subcylindrical, with slender unmodified setae in a sparse dorsal field. Prefemur about half length of telopodite, latter curved dorsomesad with three apical processes, **a** slender and recurved laterad, **b** and **e** missing, **c** enlarged and laminate, **d** small and etiolated, arising from a broadened area just

proximal to **c** on the mesal side (Figs 4 and 9). Formula: **a, C, d**. Collum broadest in front of midlength, but anterior corners not projecting. Paranota large, anterior edges strigilate (in at least one species), posterior finely crenulate, ozopores placed near center of paranotal surface. Epiproct large, notably “tridentate” with caudolateral and median tubercles enlarged (Fig. 6). Legs long, podomeres slender (fig. 7).

Comments: This genus was proposed with two species, *H. everettii* and *H. hosei*. In 1921 an additional species *H. lamprus* was added by R. V. Chamberlin, with no further locality than “Borneo.” Although the general body form is similar in all three of these species, the gonopod structure clearly reflects such a sharp dichotomy that separate generic status is mandated for the last two species mentioned.

Previous descriptions of species in this and related genera have referred to the anterior paranotal edges as “crenulate”, “finely serrate”, “serrulate”, or “kerzbahnig”. These terms are misleading in their implication of a single series of surface irregularities when, in fact, if the paranota are examined with sufficient magnification, the anterior edge is seen to be distinctly thickened and invested with a multiserial field of minute spicules (Fig. 5). The effect is quite similar to the condition already noted and designated as the *strigilus* (Hoffman, 1962) in *Polylepisus campanulae* and since observed in numerous Neotropical species of Euryurinae. Within the Bornean fauna, the character is apparently a synapomorphy of *Hoplurorhachis*, *Creagronopus*, and *Sabarhacus*, reflecting the similarities in gonopod structure. I have not observed it in genera of the tribe Psaphodesmini, such as *Parazodesmus*, *Zodesmus*, and *Ozorhacus*.

The identification of one of the telopodite processes is not asserted with confidence. Although tentatively labeled as **d** on the drawings, it might as readily be **b**, carried out of normal position by an evident rotation of the distalmost telopodite region. Future studies of different species may cast some light on this point.

Distribution: Known only from Brunei (and “N.W. Borneo”, presumably Sabah).

Name: From the Greek *hoplos* (armed) + *uros* (tail) + *rhachis*, a common combining element in this family. Gender feminine.

Species: Three nominal species are referred to this genus.

KEY TO THE SPECIES OF *HOPLURORHACHIS*

- 1. Ozopores of midbody segments located posterior to midlength of paranota and about one peritrematic diameter from lateral edge; sterna with four polished knobs. . . . . *crassipes* (Carl)
- Ozopores of midbody segments located near center of paranota, and at least four peritrematic diameters from lateral edge; sterna with four long sharp caudally declined spines . . . . . 2
- 2. Small species, body width 10.5 mm at midlength; process **c** of gonopod narrower, parallel-sided, apically truncate (Fig. 8) . . . . . *oeceter* sp. n.
- Larger species, body width 13 mm; process **c** of gonopod a broad, suboval, apically rounded lobe (Fig. 3) . . . . . *everetti* Pocock

***Hoplurorhachis everettii* Pocock**

Figs 2, 3

*Hoplurorhachis everettii* Pocock, 1897: 437, figs 12, 12a. Three male syntypes [BMNH 1895.11.4.2-4] from "N.W. Borneo", A. Everett leg. One of the males (1895.11.4.2) has been labeled as lectotype of this species; the gonopod structure of this individual is illustrated.

*Platyrhacus (Pleorhacus) everettii*: Attems, 1914: 264.

*Platyrhacus (Psaphodesmus) everettii*: Attems, 1938: 279.

Material: The male lectotype and two male paralectotypes were examined in the British Museum (Natural History), London (currently called "The Natural History Museum"). These specimens carry no data except "N.W. Borneo" but probably originated in either Brunei or Sarawak.

Description (adapted from Pocock): Dorsum black or piceous, the dark color extending laterad to but not around the peritremata, all three margins of paranota thus broadly yellowish, as are the antennae, legs, and projections of the epiproct.

Terga finely granular to coarsely coriaceous; three rows of small tubercles evident, those of the 3rd row largest.

Anterior edge of paranota of midbody segments thickened, the anterolateral angle rectangularly rounded; posterior edge finely crenulate, forming straight line with median posterior edge of tergum, produced basally into a triangular lobe; caudolateral angle subacute; ozopore removed from lateral edge by distance about 4X diameter of a peritreme. All paranotal edges entire, nearly straight, the anterior strigilate.

Gonopod structure (drawn from lectotype) as shown (Figs 2, 3): coxal setae sparse, slender, not apically penicillate; process **c** of telopodite broad, apically rounded, originating very close to **a**.

***Hoplurorhachis crassipes* (Carl) comb. n.**

Fig. 4

*Platyrhacus crassipes* Carl, 1909: 253, fig. 19. Male holotype (location, if extant, unknown) from "Borneo" without further locality.

*Platyrhacus (Pleorhacus) crassipes*: Attems, 1914: 267.

*Platyrhacus (Psaphodesmus) crassipes*: Attems, 1938: p. 277, fig. 315.

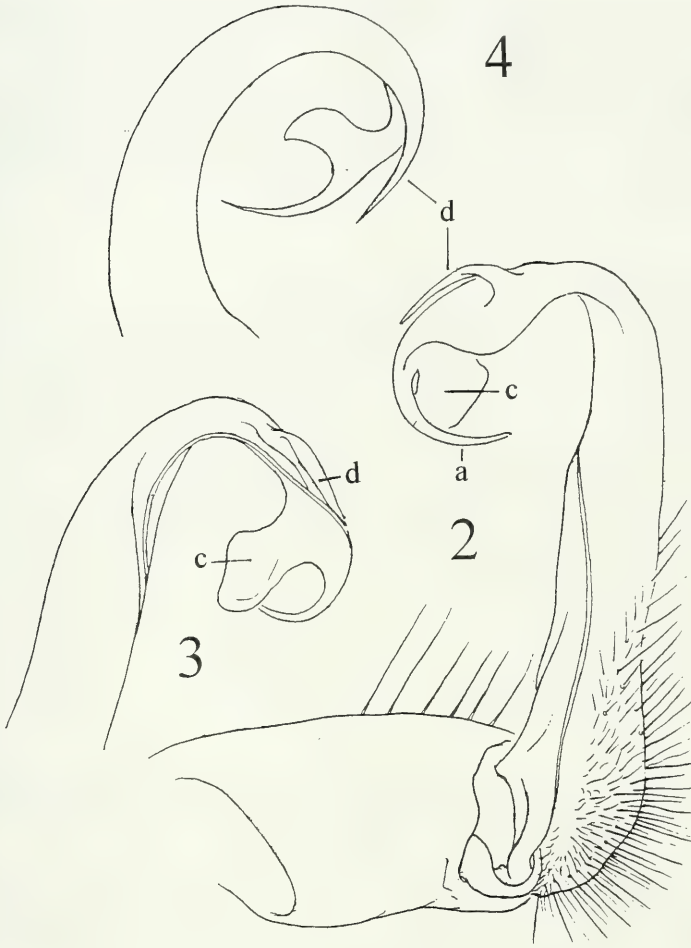
The holotype of this species has not been found in the Geneva collection. Carl's description and gonopod drawing are so precise, however, as to leave no doubt whatever about the systematic position of *crassipes*. The strongly reduced sternal spines seem to be a significant specific character for later recognition. The parts of Carl's original description that do not apply to all members of this genus are reproduced below (loose translation by author):

"Uniformly brown, basal podomeres and outer part of paranota yellowish-brown.

Collum narrow, not wider than the head, with small triangular depressed lateral lobes; a row of flat tubercles along anterior margin, a wide, shallow, transverse groove between posterior base of lateral lobes, posterior edge with a large tubercle on each side, dorsal surface rather thickly granulate with scattered larger flattened tubercles.

Metazona with dense flat granules, somewhat larger on paranota than mid-dorsum, granulation becoming finely and fainter from front to back. Posterior row of





FIGS 2-4

Fig. 2. *Hoplurorhachis everettii* Pocock, left gonopod of male lectotype (BMNH). Fig. 3. The same gonopod, distal half of telopodite, dorsal aspect. Fig. 4. *H. crassipes* (Carl), distal half of telopodite of gonopod of holotype, redrawn from Carl, 1909.

tubercles most distinct on anterior segments and becoming weaker posteriad; first two rows appear first on posterior segments.

Ozopores large, placed behind midlength on paranota and near their lateral edge, hardly more than a peritreme diameter removed from the latter.

Epiproct broad, shovel-shaped, with weakly convex posterior edge, convex lateral edges, and rounded posterior corners, somewhat constricted at the base; dorsal side sparsely granular, with two longitudinal swellings ending in a bristle. Hypoproct

with two very small paramedian tubercles. Sterna glabrous, with sparse fine granules and four low, polished projections.

Length of male 57 mm, collum 6.5 mm, 11.segment, 11.5 mm, 18th, 9 mm."

Despite the differences noted in pore location and reduction of sternal armature, Carl's drawing of the gonopod of this species (reproduced here as Figure 4) so closely resembles the form seen in *hosei* and *oeceter*, there can be little doubt that *crassipes* is congeneric with them.

***Hoplurorhachis oeceter* sp. n.**

Figs 5-9

Material: Male holotype and male paratype (MHNG) from **East Brunei**: Bangar, Bukit Patoi Nature Reserve, 60-300 m, 24 October 1988, B. Hauser leg. (field no. Bru-88/37).

Name: Approximate Latinization of the German surname Hauser ("householder" in English), bestowed in recognition of the collector's contributions to knowledge of the soil and litter arthropods of Borneo.

Diagnosis: Distinguished from the known related forms by the characters stipulated in the foregoing key to species.

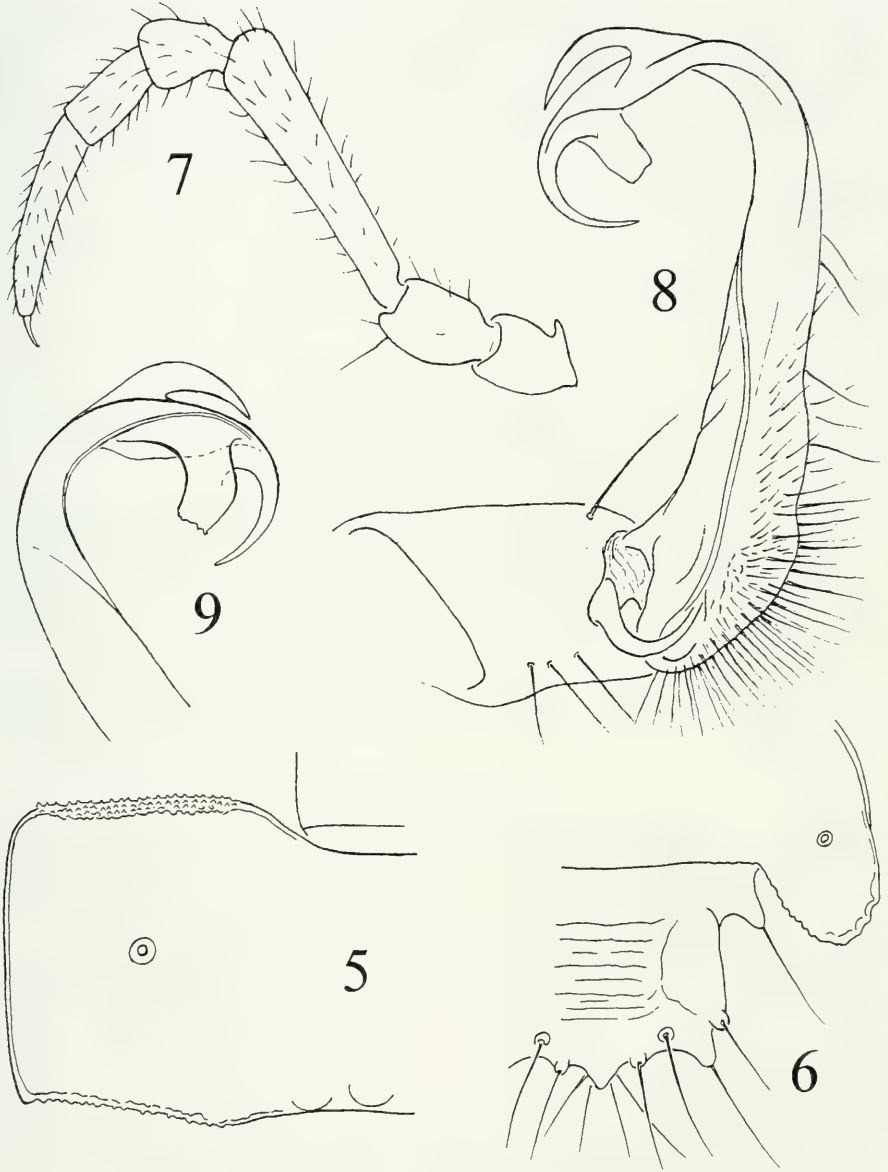
Holotype: Length ca. 62 mm (specimen broken), width/length ratio ca 18% at midbody; widths of selected segments

1 - 5.8 mm	10 - 10.9 mm
2 - 8.5	12 - 10.8
4 - 9.9	14 - 10.7
6 - 11.0	16 - 10.4
8 - 11.0	18 - 8.5

Dorsal color generally uniform, light brown, outer two-thirds of paranota, distal half of epiproct, antennae, and legs yellowish.

Epicranium coarsely granulate, with 3-2 setae in transverse series, rims antennal sockets high and prominent medially, lower ventrad and dorsad, genae with shallow median depression. 4+4 frontal hairs, 2+3 clypeal, 5+5 labral, 2+2 lower genal, all these hairs in fascicles as usual. Width of head across genae equal to transmandibular width. Antennae short and robust, unmodified.

Collum widest near anterior corner, posterolateral quadrant strongly elevated, forming transverse ridge bearing 6-6 prominent polished tubercles in a curved row along the edge; 5-5 low and indistinct tubercles along front margin; surface finely tuberculate-microcoriarius. Surface of 2nd metatergum granular, caudal edge elevated, with 6-6 acute tubercles preceded by a transverse row of 4-4 small rounded tubercles; paranota extended beyond ends of collum, edges smooth except for two blunt lateral projections. Metatergum of 3rd segment with 7-7 tubercles, surface of paranota nearly smooth. Paranota of 5th and subsequent segments about 50% larger than 3rd and 4th; dorsal surface of these segments increasingly granulose posteriad, caudal edge of metaterga becoming gradually lower until plane with prozona at midbody. Shape of paranota at midbody as in Fig. 5. Epiproct of the shape shown in Fig. 6. Hypoproct lacking median projection; paramedian tubercles large and pro-



FIGS 5-9

*Hoplurorhachis oeceter*, sp. n., holotype. Fig. 5. Left paranotum of midbody segment, dorsal aspect, showing strigilate anterior margin. Fig. 6. Right side of epiproct and paranotum of 19th segment, dorsal aspect. Fig. 7. Leg from midbody segment. Fig. 8. Left gonopod, mesal aspect. Fig. 9. Distal half of telopodite of left gonopod, dorsal aspect, slightly enlarged.



minent. Podosterna moderately elevated and densely setose, each with four ventrally-directed spines, those between posterior pair of legs the larger. Legs relatively long and slender, at midbody of the form shown in Fig. 7. Lower sides of metazona with large blunt tubercle near caudal edge just above dorsal coxal condyle. Stigmata large and auriculate, their dorsal rims thickened and elevated above segmental surface, posterior stigma elongate oval and nearly centered above the coxal condyles, anterior stigma placed lower, merging with dorsal condyle and overlapping onto posterior edge of stricture.

Gonopods (Figs 8, 9) similar to those of *everettii*, from which differing in shape and position of process **c**.

***Creagronopus* gen. n.**

Type species: *Hoplurorhachis hosei* Pocock, 1897.

Name: A neologism combining the Greek word *kreagra* (meathook) with the frequently-used element “*gonopus*” (gonopod), in allusion to the shape of process **D** of the telopodite in this genus. Gender masculine.

Diagnosis: Femoroid region of gonopod greatly elongated, up to twice that in *Hoplurorhachis*, postfemoral region bent at nearly right angle to prefemoral stem, the angulation prominently broadened; process **D** greatly enlarged, falciform, extending over and beyond apex of primary stem; process **b** smaller than **a** and recurved toward it; process **c** enlarged and laminate (Fig. 12). Formula: **(a,b) C, D**.

Remarks. The nominal species recognized in this genus are so far known only from a very few specimens, and *Creagronopus* is not represented in the Geneva collections.

KEY TO THE SPECIES OF *CREAGRONOPUS*

1. Process **D** of gonopod slender, apically sinuous; process **c** shorter, not projecting beyond base of **a** as seen in mesal aspect (Fig. 10) . . . *hosei* (Pocock)
- Process **D** evenly curved apically, not sinuous; process **c** longer, extending dorsad beyond base of **a** when seen in mesal aspect (Fig. 11)  
 ..... *lamprus* (Chamberlin)

***Creagronopus hosei* (Pocock) comb. n.**

Fig. 10

*Hoplurorhachis hosei* Pocock, 1897: 437, fig. 13. Male holotype [BMNH. 1897.3. 30.14] from “Baram”, Borneo, C. Hose leg.

*Platyrrhacus hoplurorhachis* Attems, 1899: 340 (new name proposed to correct junior homonymy with *Phyodesmus hosei* Pocock, 1897, occurring when Attems transferred both into his omnibus genus *Platyrrhacus*).

*Platyrrhacus (Pleorhacus) hoplurorhachis*: Attems, 1914: 264, 268.

*Platyrrhacus (Psaphodesmus) hosei*: Attems, 1938: 280.

Material: The male holotype [BMHN]; also **Sarawak**: along the Linjar, Nibong, and Dapoi rivers, November 1932. Oxford Univ. Exped. [BMNH 1♂]; Gunung Mulu National Park, 29 July 1977. Alec Panchen leg. [VMNH 1♂], 30 July 1977, J. M. Anderson leg. [VMNH 1♀].

Remarks: Attems created several unjustified secondary homonyms in 1899 by combining all of the existing generic categories under his very inclusive *Platyrrhacus*. In 1938, however, he revived *Hoplurorhachis hosei*, presumably under the impression that placement of the earlier name *Phyodesmus hosei* in the subgenus *Acanthodesmus* removed the homonymy.

In his 1914 key to 32 species of the subgenus *Pleorhacus*, Attems brought *everettii* and *hosei* out in couplet 10, separating them by small details of paranotal structure. In a footnote, he explained that “Die von Pocock zur Unterscheidung dieser beiden Arten angegebenen Merkmale lassen vermuten, dass es sich höchstens um geringe Varietäten derselben Art handelt.” In 1938, he granted the two unchallenged specific status. In 1998, the two are in different genera, apparently a case of taxonomic inflation but in actuality only the result of examination of the type material. Attems had to rely on Pocock’s brief descriptions and minuscule drawings.

The very limited material which I have examined suggests the occurrence of either one randomly variable species in this genus, or several closely related sibling species differing more in peripheral characters than in gonopod structure. I give here comparable drawings made from the types of *hosei* and *lamprus*. Until more material is available, further speculation on these options is pointless. For the present, *lamprus* is retained as a valid name, and no new names are proposed for the different gonopod variations.

***Creagonopus lamprus*** (Chamberlin) comb. n. Figs 11, 12

*Platyrrhacus lamprus* Chamberlin, 1921: 83. Male holotype [MCZ: 4673] labeled only “Borneo”, H. W. Smith, leg.

*Platyrrhacus (Psaphodesmus) lamprus*: Attems, 1938: 280.

This species was adequately described and correctly compared with *Hoplurorhachis hosei* by its author, but in the absence of gonopod illustration, its degree of distinctness could not be estimated. Examination of the holotype permitted correction of the deficiency, and the present drawing suggests that *lamprus* is at least subspecifically distinct in the ways verbalized in the foregoing key. However, since comparison is being made only between two single males, it seems possible that only normal intrapopulational, rather than geographic, variation is being expressed. Regrettably, no precise locality is known as the provenance of *lamprus*.

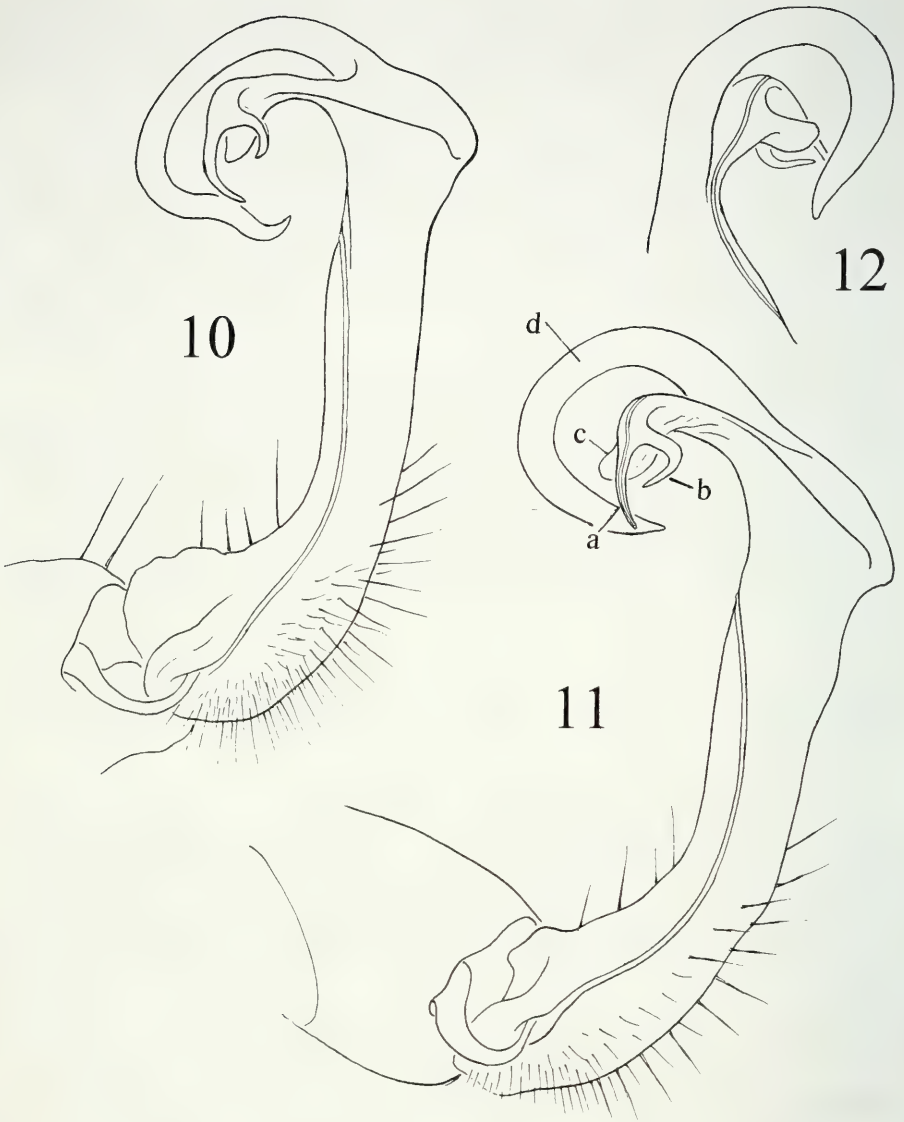
***Sabarhacus*** gen. n.

Type species: *S. derodontus* sp. n.

Name: A neologism composed of the elements “Saba-” (from Sabah) + “rhacus”, a root element commonly used in genera of this family. Gender masculine.

Components: In addition to the new species described here, this genus includes *Platyrrhacus succidus* Attems, 1932 and possibly *Platyrrhacus gongylodes* Attems, 1899 (see discussion following).

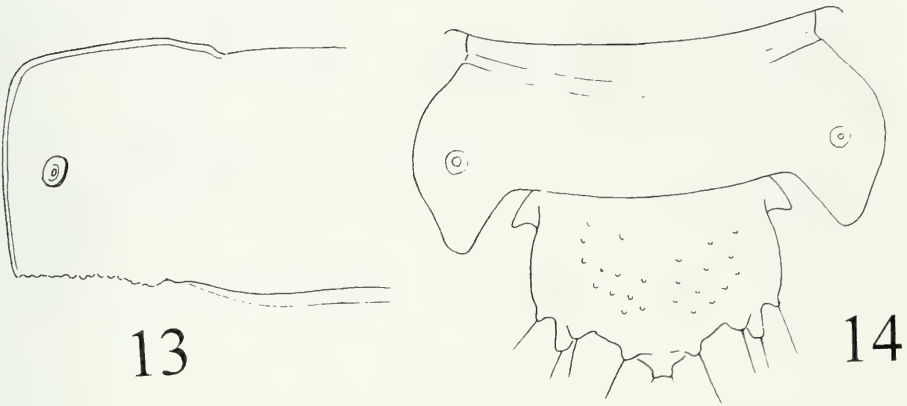
Diagnosis: Process **D** of gonopod enormously enlarged, projecting above and beyond major branch of telopodite (**a + c**); gonocoxa with dorsal and paracannular



FIGS 10-12

*Creagronopus hosei* (Pocock), lectotype (BMNH). Fig. 10. Left gonopod, mesal aspect. *Creagronopus lamprus* (Chamberlin). Fig. 11. Left gonopod, mesal aspect. Fig. 12. Distal half of left telopodite, dorsal aspect from holotype (MCZ).





FIGS 13-14

*Creagronopus* cf. *lamprus*, specimen from Mulu Caves National Park, Sarawak (VMNH). Fig. 13. Left paranotum of midbody segment, dorsal aspect. Fig. 14. Epiproct and 19th segment, dorsal aspect.

fields of unmodified macrosetae (Fig. 19); posterolateral corner of collum occupied by several triangular tubercles, anterior corner projecting acutely laterad (Fig. 15); paranota nearly square in outline at midbody; metaterga with three rows of tubercles, those of rows 1 and 2 small and widely spaced, those of 3 larger and projecting beyond caudal tergal edge. Legs distinctly shorter and stouter than in *Hopluorhachis* (cf. Figs 7 and 18).

Remarks: A species from Deli, Sumatra, named *Platyrrhacus gongylodes* by Attems (1899) may possibly be referable to *Sabarhacus*. A specimen in the Geneva collection labeled "Sumatra" and identified as *gongylodes* by J. Carl shows a lobed expansion of the gonopod apex that seems exactly homologous with process *c* of the two Borneo species. This modification is not shown in Attems' illustration of the holotype, which now must be examined in this context. If the two specimens are not conspecific, there remains the possibility that the one considered by Dr. Carl to be *gongylodes* was mislabeled and actually came from Borneo. Lastly, of course, it is not impossible that *Sabarhacus* is represented by endemic Sumatran species.

KEY TO SPECIES OF *SABARHACUS*

- 1. Outer half of paranota yellowish; antennae brown; posterior margin of collum with about 15 enlarged tubercles, ozopores located near midlength of paranota; gonopods as in Fig. 21. . . . . *sucidus*
- Outer two-thirds of paranota yellowish; antennae yellow; posterior margin of collum with about eight enlarged tubercles; ozopores (at mid-body) located posterior to midlength of paranota; gonopods as in Fig. 19 . . . . . *derodontus*

*Sabarhacus sucidus* (Attems) comb. n.

Fig. 21

*Platyrhacus sucidus* Attems, 1932. Treubia, v. 14, p. 34, figs 12-15. Syntypes [NMW] labeled only "Soela Inseln" [a variant spelling of "Sulu Islands"].

*Platyrhacus (Psaphodesmus) sucidus*: Attems, 1938: 278, figs 317, 318.

I have examined type material of this species at Vienna, and prepared a new gonopod drawing for contrast with those of *S. derodontus*; unfortunately I did not illustrate other characters, and must infer some differences with *derodontus* on the basis of the published description. Gonopod structure is much the same in the two taxa, and more numerous diagnostic features occur in body form, such as coloration of the antennae and paranota, tuberculation of the collum, and location of the ozopores, as mentioned in the foregoing key.

Attems' drawings of the gonopod (1932: Figs 14, 15) appear to have been made from a slide preparation which deformed the normal position of the apical branches. I give here (Fig. 21) a new drawing which shows the correct formation of the appendage.

*Sabarhacus derodontus* sp. n.

Figs 15-20

Material: Male holotype [MHNG] from **Sabah**: Sandakan Residency: Kabili-Sepilok Forest Reserve, in lowland dipterocarp forest. B. Hauser leg. 22 April 1982 (field no. Sab-82/2).

Name: Neologism composed of the Greek terms *deiros* (neck) + *odontos* (tooth), in reference to the prominent dentations on lateral margins of collum. Gender masculine.

Diagnosis: Anterolateral corner of collum acutely angular instead of a rounded lobe, posterolateral with three prominent dentations (the enlarged outermost members of the usual posterior marginal series) (Fig. 15); ozopores located in posterior third of paranotal length (Fig. 16); setae of gonocoxae unusually large and robust (Fig. 19).

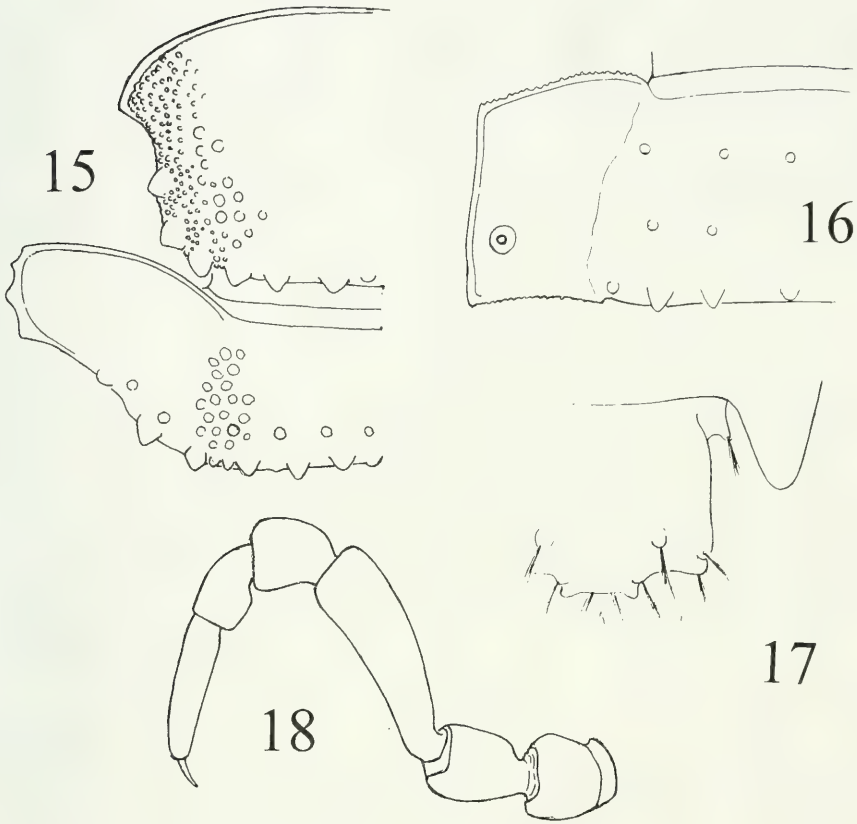
Holotype: Adult male, length ca. 62 mm (specimen broken), width/length ratio ca. 18%; widths of selected segments:

1 - 5.8 mm	10 - 10.9 mm
2 - 8.5	12 - 10.8
4 - 9.9	14 - 10.7
6 - 11.0	16 - 10.4
8 - 11.0	18 - 8.5

Dorsal color generally uniform light brown, with outer two-thirds of paranota, distal half of epiproct, antennae, and legs yellowish.

Epicranium coarsely granulate, with 3-2 setae in transverse series, rims of antennal sockets high and prominent on median side, lower ventrad and dorsad; genae with shallow median depression. 4+4 frontal hairs, 2+3 clypeal, 5+5 labral, 2+2 lower genal, these hairs all fasciculate as usual. Width of head across genae = to transmandibular width. Antennae short and robust, without evident modification.

Collum (Fig. 15) widest near anterior corner, posterolateral quadrant strongly elevated, forming transverse ridge bearing 6+6 prominent tubercles in a curved row along edge; 5+5 low and indistinct tubercles along front margin; surface finely

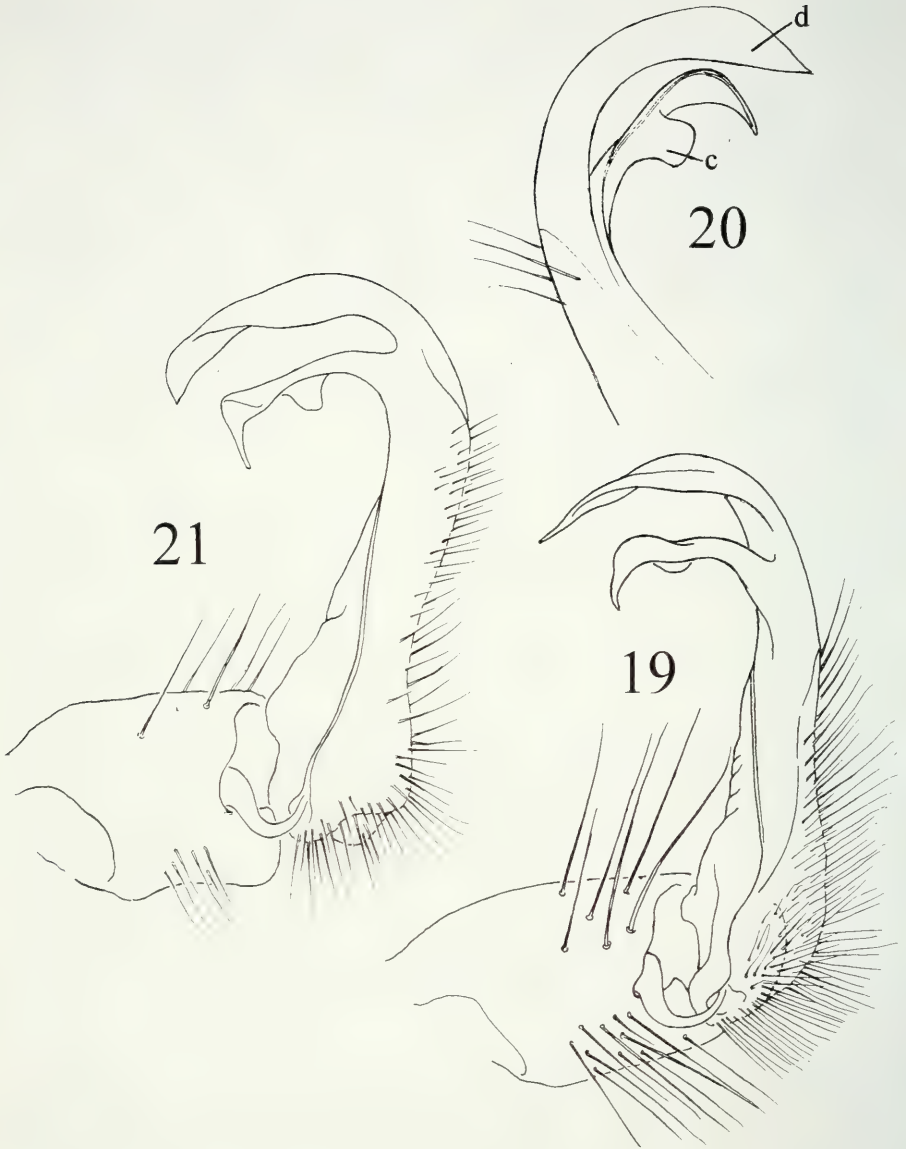


FIGS 15-18

*Sabarhacus derodontus*, sp. n., holotype (MHNG). Fig. 15. Left side of collum and 2nd body segment. Fig. 16. Left paranotum of midbody segment. Fig. 17. Right side of epiproct, dorsal aspect. Fig. 18. Leg from midbody segment (setae omitted).

tuberculate-microcoriarius. Surface of 2nd metatergum granular, caudal edge elevated, with 6+6 tubercles (Fig. 15) preceded by a transverse row of 4+4 small rounded tubercles; paranota extended beyond ends of collum, edges smooth except for two blunt lateral projections. Metatergum of 3rd segment with 7+7 tubercles, dorsum of paranota nearly smooth. Surface of segments 4-19 becoming increasingly granulose caudally, caudal edge of these terga also becoming lower until even with prozona near midbody. Paranota of segments 5 *et seq.* about 50% larger than those of 3rd and 4th segments. Profile of paranotum of midbody segment, Figure 16.

Epiproct as illustrated (Fig. 17), marginal setae compound/fasciculate; hypoproct large with two large apical paramedian tubercles, the edge between their bases straight. Podosterna moderately elevated, densely setose; acute, ventrally directed



FIGS 19-21

*Sabarhacus derodontus*, sp. n., holotype (MHNG). Fig. 19. Left gonopod, mesal aspect. Fig. 20. Distal half of left telopodite, dorsal aspect. *Sabarhacus succidus* (Attems), holotype (NMW). Fig. 21. Left gonopod, mesal aspect.



subcoxal spines present, those of posterior legpair distinctly larger. Dorsal coxal condyles large, anterior stigmata prominent, dorsally auriculate, posterior stigmata slightly smaller, elongate-ellipsoid, not notably auriculate, placed almost equidistant between coxal condyles; small setose knob just dorsad to each posterior dorsal condyle. Legs relatively short and stout (Fig. 18), unusually hairy: setae of anterior legs virtually as long as diameter of podomeres.

Gonopods (Figs 19-20) similar to those of *sucidus*, process **D** more acuminate apically, process **c** less conspicuous, apex of telopodite evenly curved (mesal aspect) rather than bent at right angle.

### Tribe **Phyodesmini** Cook

*Phyodesmini* Cook, 1896: 4 (as subfamily).-- Hoffman, 1980: 163 (as tribe).

Diagnosis: Large to very large species (length of males to about 110 mm). Collum broadest across front edge, anterior corners often produced forward as rounded lobes. Meteterga smooth to coriaceous, with transverse series of obscure tubercles. Paranota (Fig. 22) large, set high on body and nearly horizontal, lateral edges deeply incised, anterior corner usually projecting further laterad than posterior. Gonopods very large, telopodites long, nearly straight, parallel to each other, without torsion, the prostatic groove visible for most of its length in mesal aspect, ending on a small digitiform solenomere; prefemoral region very elongated, comprising up to two-thirds length of telopodite.

Component: *Phyodesmus* Cook, 1896.

### *Phyodesmus*

*Phyodesmus* Cook, 1896: 1. Described with one species. Type species: *Polydesmus pictus* Peters, 1864, by monotypy and original designation.-- Hoffman, 1978: 245 (revision).

Diagnosis: With the characters of the tribe.

Components: *P. longispinosus* (Silvestri, 1896), *P. scutatus* Peters, 1864), *P. sublimbatus* (Silvestri, 1897), *P. laticlavus* Hoffman, 1978, *P. pictus* (Peters, 1864), *P. hosei* Pocock, 1897, *P. ornatus* Pocock, 1897, *P. magnificus* (Silvestri, 1896).

Range: The genus is autochthonous in southwestern Borneo.

Remarks: My revision (1978) of this group of striking millipeds clarified the status of most names referable to it, but left unsettled both the systematic position of the genus and the status of the several species of the "*Pictus* Group".

Despite the great size and marvelous colors of these animals, there are remarkably few specimens available with precise locality data, and until this situation is alleviated, the relative status of the names *ornatus*, *pictus*, and *magnificus* will remain uncertain. I still have no insights into the relationships of the genus. The possibility may be noted, that what I referred to as the "ensiform process" of the gonopod may be homologous with "process **d**" that is readily recognized in the Psaphodesmini of the Papuan Region.

*Phyodesmus magnificus* (Silvestri)

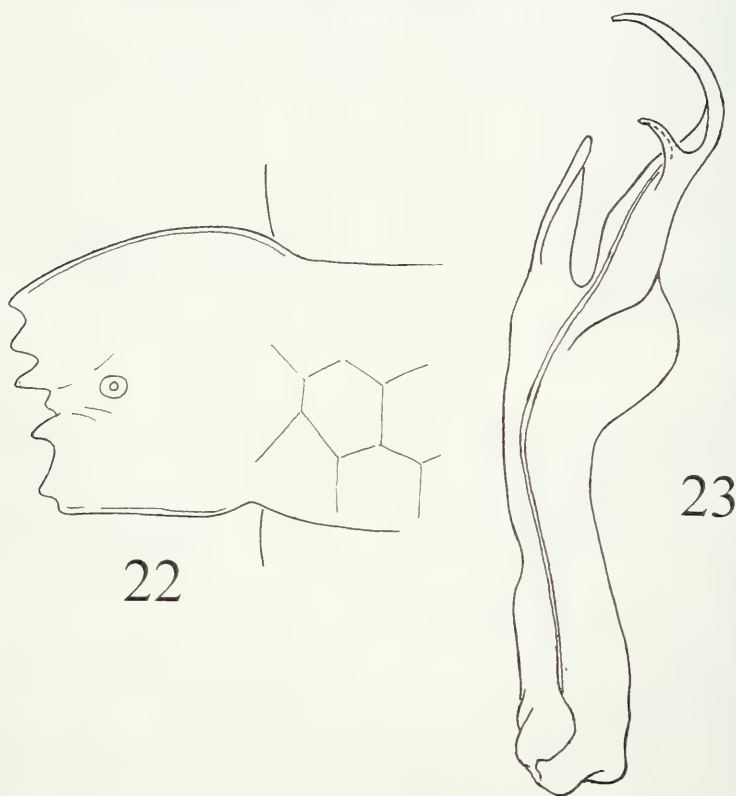
Fig. 23

*Platyrrhachus magnificus* (Silvestri, 11896: 23, fig. 3. Holotype male [MCSNG] from "Sarawak".

*Phyodesmus magnificus*: Cook, 1896: 4 --Hoffman, 1978: 254, fig. 15.

Material: **Sarawak**: Sabal (Forest Reserve Station), southeast of Serian, 180 m, 10 December 1987, B. Hauser leg. (MHNG Sar- 87/71, 2♂♂).

The recently-preserved material retained much of its original coloration when examined in October of 1991. The metaterga are slaty-blue, each with a middorsal orange-ochre marking, widest posteriorly, extending the entire metatergal length and continued onto the prozonum as a much narrower, triangular, yellow median marking. Prozona black dorsolaterally, with a rounded white spot in front of paranotal base. Dark prozonal color extends caudad onto metazonum in three digiform lobes which



FIGS 22, 23

*Phyodesmus magnificus* (Silvestri). Fig. 22. Left paranotum of midbody segment, specimen, specimen from southeast of Serian, Sarawak (MHNG). Fig. 23. Left gonopod, mesal aspect, from holotype (MSNG).

lack the appended small round black spots that usually appear in specimens of *P. ornatus*.

The specimens follow the key to species in my 1978 revision without difficulty, and the gonopod structure agrees well with that of the holotype (Fig. 23), which I studied and illustrated at Genoa in 1975.

Tribe **Platyrhacini** Pocock

*Platyrhacini* Hoffman, 1980: 163 (as tribe). Nomen correctum et translatum ex Platyrhachidae Pocock, 1895.

*Acanthodesmini* Cook, 1897: 4 (as subfamily).

Components: *Acanthodesmus* Peters, 1864; *Arbelorhacus* gen. nov.; *Barydesmus* Cook, 1896; *Eurydirorhachis* Pocock, 1897; *Nyssodesmus* Cook, 1896; *Platyrhacus* Koch, 1847; *Rhyphodesmus* Cook, 1896; *Stenoniodes* Pocock, 1897; and *Tiroademus* Cook, 1896.

Diagnosis (Borneo taxa only): A probably polyphyletic group of genera distinguished from Phyodesmini by gonopod shape and from Hoplurorhachini by structure of the paranota and epiproct as stated in the foregoing key. Gonotelopodite with two distal branches (**a, d**, or **a, b**) or three (**a, b, c**).

Remarks: The present composition of this taxon is by no means asserted as monophyletic, and future studies may show the desirability of segregating the Neotropical genera (*Barydesmus*, *Nyssodesmus*, and *Tiroademus*) into a discrete tribe. *Platyrhacus* in its restricted sense (typified by *P. fuscus* Koch) is widespread in Java, Sumatra, and the Malay peninsula, where the species express considerable diversity in body form, less so in gonopod structure, which is essentially identical with that of the nominal genus *Stenoniodes* (see comments under that generic heading). Despite its disjunct occurrence in Guyana [olim British Guiana], the single species of *Rhyphodesmus* (*druryi* Newport, 1844, with the synonyms *terminalis* Cook, 1897, and *amphelictus* Chamberlin, 1921) has a genitalic structure like that of *Platyrhacus*, and the possibility exists that it is an Indomalayan species transported by commerce into Guyana. It has not, however, been rediscovered in southeast Asia despite its large size.

KEY TO BORNEAN GENERA OF *PLATYRHACINI*

1. Sterna without subcoxal spines; process D of gonopod long, broad, very thin, resembling a curved knife blade; epicranium with a distinct smooth transverse belt immediately preceding from edge of collum . . . . . *Arbelorhacus*
- Sterna with an acute ventral spine subtending base of each coxa; epicranium without distinct transverse smooth band . . . . . 2
2. Paranota of segments 2-4 small and narrowed, much smaller than at midbody; front edge of collum medially elevated and reflexed above level of epicranium (Fig. 24); epiproct spatulate, not notably constricted at base, posterior corners rounded (Fig. 33); legs long (Fig. 25); gonopods short, massive, the two processes **a** and **d** curved dorsal and then laterad, subparallel to each other (Fig. 26) . . . . . *Stenoniodes*

- Paranota of segments 2-4 large and horizontal, nearly as broad as those at midbody, latter subrectangular, posterior corner acute or projecting anterior edge of collum not abruptly elevated above adjacent surface of head; epiproct short, constricted basally, broadest distally (Fig. 40), posterior corners rounded; gonopods less massive, prefemoral region smaller than coxa, apical elements not as described . . . . . 3
- 3. Gonopod telopodite relatively short and straight, with three distal processes (Fig. 39) . . . . . *Acanthodesmus*
- Gonopod telopodite long and curved, with two distal processes (Fig. 46) . . . . . *Eurydirorhachis*

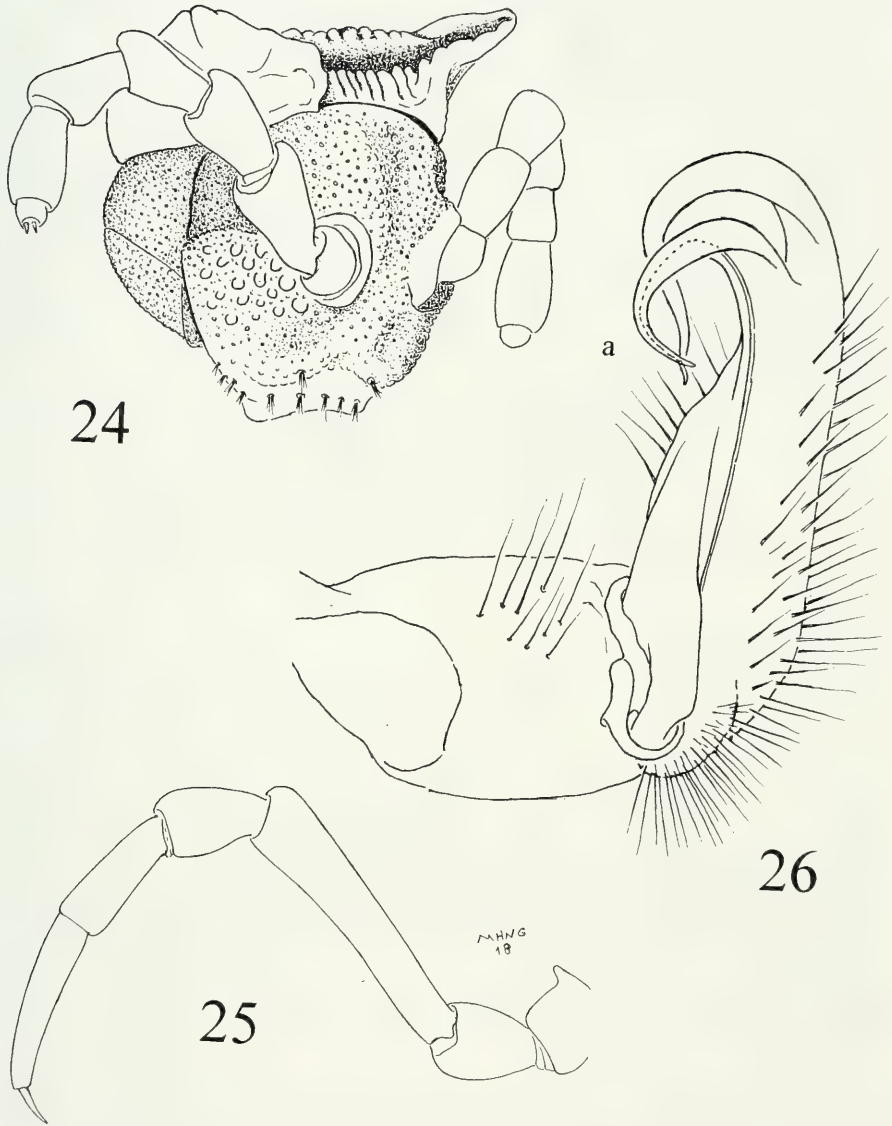
### *Stenoniodes*

*Stenoniodes* Pocock, 1897: 430. Described with four new species. Type species: *Stenoniodes catorii* Pocock, by original designation. – Hoffman, 1980: 163.

Diagnosis: Collum small, trapezoid, broadest across anterior edge, median section of latter abruptly elevated above head surface and reflexed caudad (Fig. 24), anteriormost paranota elevated about 45° above horizontal, narrow and widely separated from each other, their apices rounded; paranota at midbody narrow, widely separated, laterally rounded, peritreme set in about midsurface (Fig. 32); legs long and relatively slender (Fig. 25). Gonopods short and massive, the setose prefemoral region about equal in size to coxa, process **a** small, slender, curved dorsal and then laterad into about a half-circle; process **b** larger than **a** and curved more or less subparallel to it (Fig. 26).

Remarks: Knowledge of this genus is unsatisfactory in two respects. One is that its status vis-à-vis *Platyrhacus* itself in the Malaya-Sumatra-Java region requires clarification. These two nominal genera cannot be maintained on gonopod structure alone, but the general body form of *Stenoniodes* – the small, modified collum, wide slender paranota, and long legs – argues that some supraspecific level of differentiation has been achieved by the Borneo contingent. Until the composition of *Platyrhacus* itself has been thoroughly reviewed, it seems justifiable to continue recognition of *Stenoniodes*. A more complicated problem, one less amenable to an arbitrary solution, is the status of the various specific names that have been based on members of this group. Pocock set up the genus to contain five new species, three of them from Sandakan, which he distinguished primarily by appeal to coloration, size, shape of collum, and similar peripheral details, all of these bases for distinction being only relative. Gonopodal differences were cited in only a secondary sense, and these appendages were illustrated only for two of the species. Since all of Pocock's named forms were known from one or two specimens only, it was difficult to distinguish actual specific differences from those attributable to normal intraspecific variation. Subsequent additions to the genus by Attems (e.g., 1932) were made without reference to the existing Pocockian names, and only intensified the confusion. It is remarkable that in the description of *Platyrhacus benganus*, for instance, Attems (1932: 31) compared the new species only to four in Sumatra and a fifth restricted to Guyana. Had he given the slightest attention to Pocock's 1897 paper, he could





FIGS 24-26

*Stenoniodes creaghii* (Pocock), specimen from Sepilok, Sabah (MHNG). Fig. 24, oblique anterolateral view of head and collum. Fig. 25, Leg from midbody segment, showing elongated podomeres. Fig. 26, Left gonopod, mesal aspect.

scarcely have failed to see the near identity of the gonopod structure in *bengitanus* (Attems' Fig. 7) and *Stenoniodes angulicollis* (Pocock's Fig. 5), a Bornean species.

For these reasons, it seems desirable to attempt a survey of this nominal genus, even though it must be a very provisional one in light of the few specimens examined. In 1975 I had the opportunity to examine Pocock's types in a cursory way and prepare gonopod and collum sketches for several of them. With this reference material it has been possible to associate Dr. Hauser's Sabah material with two of the Pocock names, and to infer something about the status of those of Attems. However, an adequate revision of the genus can only be accomplished by someone able to assemble all existing material in one place for direct comparison.

The following chronological list gives the names, type localities, and type depositories of the nominal taxa which I think belong in *Stenoniodes*.

<i>Stenoniodes catori</i> Pocock, 1897	Sandakan	BMNH ♂
“ <i>angulicollis</i> Pocock, 1897	Sandakan	BMNH ♂
“ <i>creaghi</i> Pocock, 1897	“Sandakan coast”	BMNH ♂
“ <i>baluensis</i> Pocock, 1897	Mt Kinabalu	BMNH ♀
“ <i>sibutensis</i> Pocock, 1897	Sibutu Island	BMNH ♂
<i>Platyrrhacus arrogans</i> Attems, 1932	“Soela-Eiland”	NMW ♂
“ <i>bengitanus</i> Attems, 1932	Mahakam River	NMW ♂

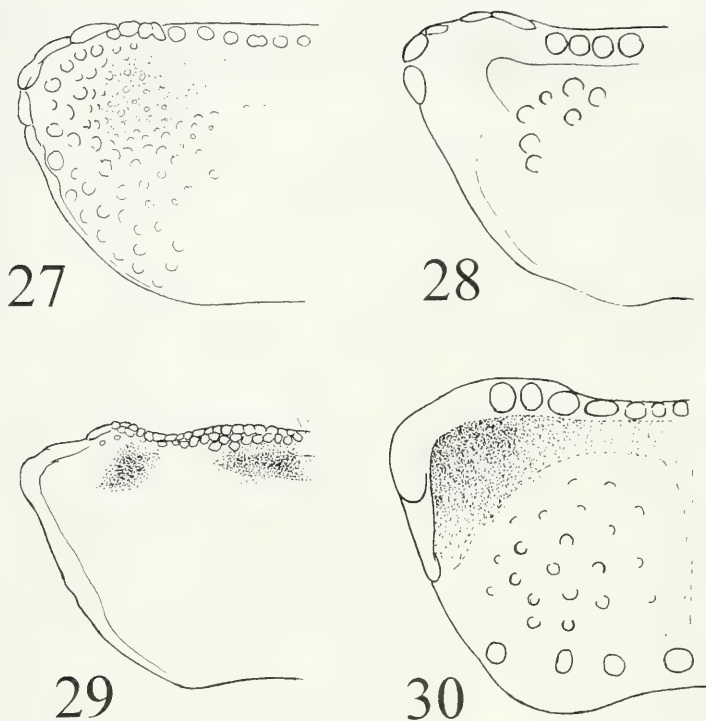
### *Stenoniodes creaghii* Pocock

Figs 24-27

*Stenoniodes creaghii* Pocock, 1897: 432, fig. 5. Male holotype [BMNH] from “North Borneo, Sandakan coast.”

Material: Male [MHNG] from **Sabah**: Sandakan Residency: Sepilok, on the road between “Forest Research Center” and “Orange-Utan Rehabilitation Station”, 22 April 1982, B. Hauser leg. (field no. Sab-82/1). Male [MHNG] from **Sabah**: Sandakan Residency: Sepilok, “Kabili-Sepilok Forest Reserve”, in forest near “Orange-Utan Rehabilitation Station”, 22 April 1982, B. Hauser leg. (field no. Sab-82/2). Female [MHNG] from **Sabah**: Sandakan Residency: Sepilok, near “Forest Research Center”, 2 May 1982, B. Hauser leg. (field no. Sab. 82/24). Two males [MHNG] from **Sabah**: Sandakan Residency: Sepilok, “Kabili-Sepilok Forest Reserve”, in forest near pond, 3 May 1982, B. Hauser leg. (field no. Sab-82/25). Male [MHNG] from **Sabah**: Sandakan Residency: Sepilok, “Kabili-Sepilok Forest Reserve”, in forest near “Orange-Utan Rehabilitation Station”, 3 May 1982, B. Hauser leg. (field no. Sab-82/26). Two males from **Sabah**: Sandakan Residency: Sepilok, “Kabili-Sepilok Forest Reserve”, in forest near “Orange-Utan Rehabilitation Station”, path to mangrove before the “Ridge”, 6 May 1982, B. Hauser leg. (field no. Sab-82/30).

Remarks: A male specimen at hand concurs well with the original description and drawings. The gonopod structure differs from that in *angulicollis* in the presence of numerous setae in a dorsal coxal field (against only three or four, as well as in the course of the prostatic groove as seen in mesal aspect (cf. Figs 26 and 34). In *creaghii* the primary telopodite stem faces more directly mesad, so that the groove runs continuously up the mesal side of its base; in *angulicollis* the stem is basally more turned dorsal, so that the groove curves around to the dorsal side and is less visible in mesal aspect. Of course the much longer and more sinuously curved process **d** is an additional feature of *creaghii*.



FIGS 27-30

Fig. 27. *Stenionodes creaghii* Pocock, specimen from Sepilok, Sabah. (MHNG), left half of collum, dorsal aspect. Fig. 28. *Stenionodes angulicollis* Pocock, holotype (BMNH), left half of collum. Fig. 29. *Stenionodes catorii* Pocock, holotype (BMNH), left half of collum. Fig. 30. *Stenionodes baluensis* Pocock, holotype (BMNH), left half of collum. Drawings to same scale.

### *Stenionodes angulicollis* Pocock

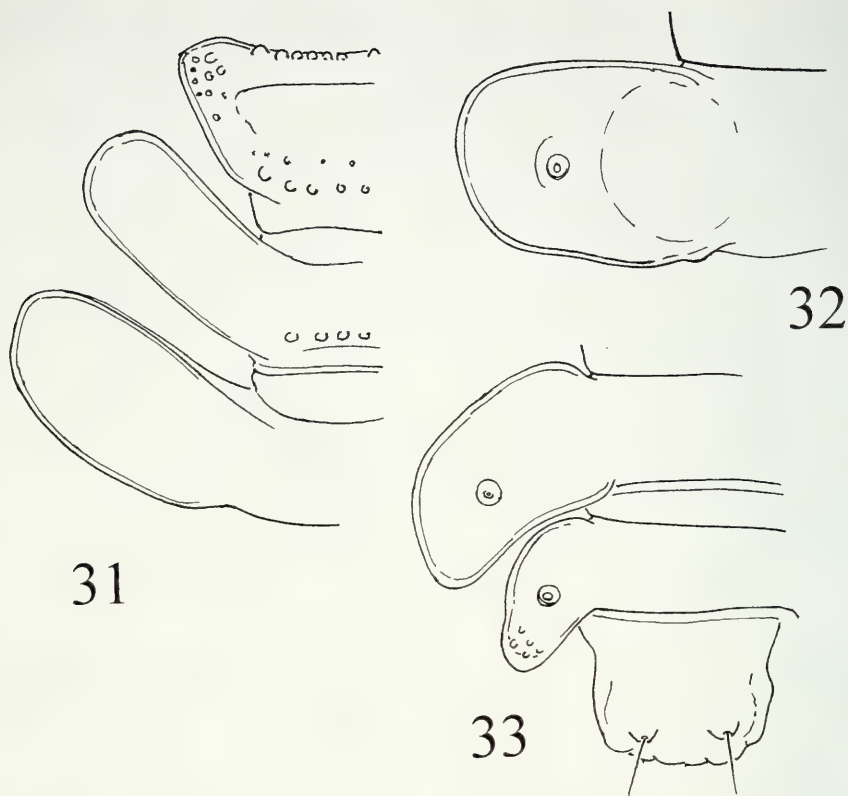
Figs 28, 31-34

*Stenionodes angulicollis* Pocock, 1897: 432. Male holotype [BMNH!] from "Sandakan" without further locality.

*Platyrrhacus bengitanus* Attems, 1932:30, figs 5-7. Male holotype [NMW] from Ben Gitan on the Mahakam River, Kalimantan. **New Synonymy!**

Material: Male [MNHG] from **Sabah**: Interior Residency: road to Kimanis, 10 miles from Keningau, in secondary forest at 1170 m, 13 May 1982, D. Burkhardt leg. (field no. Sab-82/51). Male [FMNH] from **Kalimantan**: Nunukan Island, East Kalimantan District, January 1934, R. von Hentig leg. Three males [VMNH] from **Sarawak**: vicinity of Mulu caverns, Gunung Mulu National Park, 1977-1978, J. G. E. Lewis & P. J. Chapman leg. Male type of *bengitanus* [NMW] from **Kalimantan**: Ben Gitan, Mahakam River.

Remarks: Examination of Attems' type specimen of *bengitanus* in the Vienna collection confirms the suspicion, based on the original gonopod drawings of this species and *angulicollis*, that these two names are strictly synonymous.



Figs 31-33

*Stenoniodes angulicollis* Pocock, specimen from Nunukan Island, Kalimantan (FMNH). Fig. 31. Left half of collum and segments 2 and 3, to show anterior reduction in width. Fig. 32. Paranotum of midbody segment. Fig. 33. Epiproct and left paranota of segments 18 and 19.

***Stenoniodes arrogans* (Attems) comb. n.**

*Platyrhacus arrogans* Attems, 1932: 29, figs 1-4. Male holotype [location unknown, perhaps NMW] labeled only "Soela Inseln" [a variant spelling of Sulu Islands, presumably the archipelago between Borneo and Mindanao].

If my interpretation of the type locality data is correct, the name *arrogans* should be contrasted with the description (or type specimen) of *sibutensis* Pocock, based on material from the same region as assumed of *arrogans*.

***Stenoniodes baluensis* Pocock**

Fig. 30

*Stenoniodes baluensis* Pocock, 1897: 433. Male holotype [BMNH] from Mount Kinabalu, Sabah.



***Stenoniodes catorii* Pocock**

Fig. 29

*Stenoniodes catorii* Pocock, 1897: 431, fig. 4, 4a. Male holotype [BMNH] from Sandakan, Sabah.

***Stenoniodes sicutensis* Pocock**

*Stenoniodes sicutensis* Pocock, 1897: 433. Male holotype [BMNH] from Sibutu Island [politically a part of the Philippines, despite close proximity to northeastern Borneo].

***Acanthodesmus***

*Acanthodesmus* Peters, 1864: 547. Proposed as a subgenus of *Polydesmus*, with five species. Type species: *Polydesmus pilipes* Peters, 1864, by simultaneous subsequent designation of Silvestri, 1896, and Cook, 1896. – Hoffman, 1980: 164; 1984: 254 (revision).

Diagnosis: Medium-sized platyrhacids (length of females to 110 mm), paranota of anterior segments (especially segment 2) large and horizontal imparting a notably broadened appearance to front half of body. Paranota of midbody segments large, nearly quadrate, lateral edge with three to six rounded lobes (Fig. 36); ozopores prominent, removed from lateral edge by distance about equal to one peritrematic diameter; dorsal surface of metaterga granular, with three or four transverse rows of tubercles. Epiproct strongly constricted basad, broadest near slightly convex caudal edge (Fig. 40). Sterna typically with four spines directed ventrad or caudoventrad. Telopodite of gonopod (Fig. 37) long and slender, distally curved over (dorsally) coxa and torsate about 100° dextrad, only proximal part of prostatic groove visible in mesal aspect; typically three apical processes, formula **A, b, c**, the solenomere far larger than either of the adjunct processes.

Remarks: This genus (which is endemic to Borneo) was summarized in my 1984 revision, and no additional relevant information has come to my hand during the past 12 years. I provide here only some illustrations of the type species *pilipes* and a list of the known species. Since the species are distinguished by subtle differences in gonopod structure, no key is attempted and investigators are referred instead to the drawings in the revision.

The overall similarity in genitalic structures suggests the possibility of only a subspecific level of differentiation, a point to be considered when more material with accurate collection data becomes available. It is astonishing that all of the following species are still known only from their original type specimens; at least I have not found any material referable to this genus in museum collections examined over the past three decades.

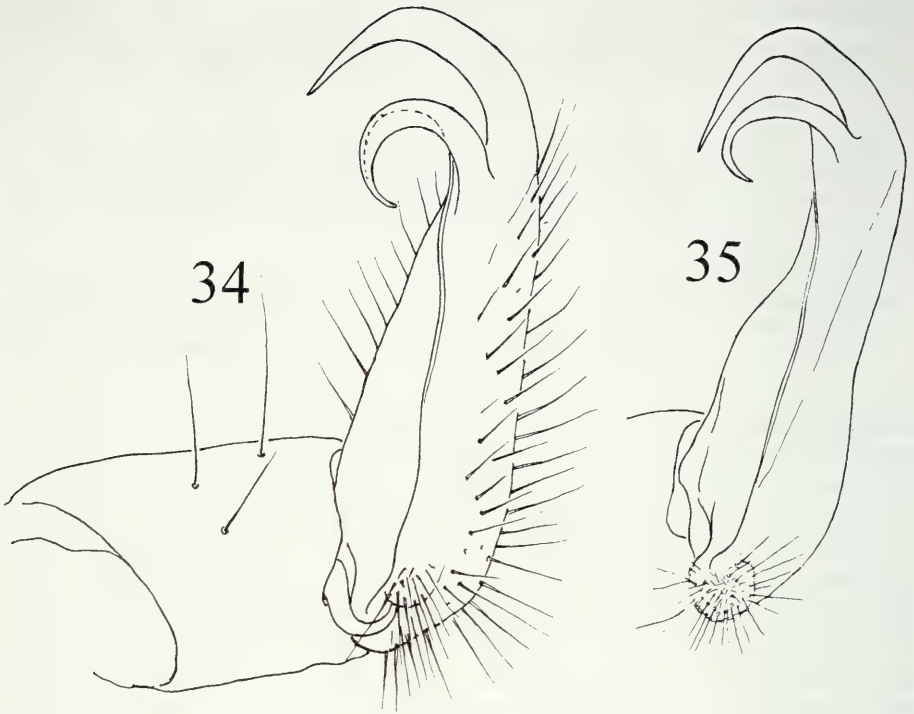
***Acanthodesmus anambasius* (Attems)**

Fig. 37

*Platyrhacus anambasius* Attems, 1932: 36, figs 16-19. Type material (NMW) from "Anambas Inseln."

*Platyrhacus (Acanthodesmus) anambasius*: Attems, 1938: 251, figs 279, 280 ("Natoena-Insel" cited as additional locality).

Attems' enigmatic species *Platyrhacus anambasius* requires consideration as a member of this genus. Until examining the holotype at Vienna in 1997, I suspected



FIGS 34, 35

*Stenoniodes angulicollis* Pocock. Fig. 34. Left gonopod of specimen from Interior Residency, Sabah. Fig. 35. Left gonopod of holotype (BMNH).

that the long acute prefemoral projection shown in the original drawings might be some kind of artifact. A very critical inspection showed that the structure is quite real, a most unusual development for this family. The remainder of the gonopod conforms so closely to the normal appearance for this genus (cf. Figs 37 and 38), that I believe the best disposition for *anambasius* is placement in *Acanthodesmus*. An additional justification for this option is the occurrence of a small "anlage" in the same position in *A. mortoni* (cf. Fig. 38).

It is not clear to me whether the reference to "Natoena" (=Natuna) Island in Attems' 1938 work represents an additional locality from which he saw material, or is merely an attempt to localize the original locality "Anambas Inseln." These two names actually apply to two separate island groups in the South China Sea.

***Acanthodesmus attenuator* (Chamberlin)**

*Platyrrhacus attenuator* Chamberlin. 1921: 84. Female holotype [MCZ] from "Ladong, Sarawak".

*Acanthodesmus attenuator*: Hoffman, 1984: 258.

Although the peripheral characters of the female holotype clearly mandate reference of the species to *Acanthodesmus*, only the examination of a conspecific male from the type locality will establish whether *attenuator* is a valid species or only a junior synonym of one of the older names.

***Acanthodesmus discrepans* (Pocock)**

*Eurydirorhachis discrepans* Pocock, 1897: 436. Holotype male [BMNH] from “Borneo” without specific location.

*Platyrhacus discrepans*: Attems, 1938: 229.

*Acanthodesmus discrepans*: Hoffman, 1984: 258.

***Acanthodesmus dorsalis* (Silvestri)**

*Platyrhachus dorsalis* Silvestri, 1896: 22. Syntypes [MCSNG] from “Sarawak” without specific locality.

*Platyrhacus (Pleorhacus) anthropophagorum*: Attems, 1914: 267. New name for *P. dorsalis*, ipso facto with the same type specimens.

*Acanthodesmus dorsalis*: Hoffman, 1984: 258, figs 8, 9.

Attems proposed *anthropophagorum* (“of the man-eaters”) to replace the homonymy resulting from his inclusion of Peter’s older name *dorsalis* in *Platyrhacus*. However, the homonymy is only secondary because Peter’s *dorsalis* had never been associated with *Platyrhacus* prior to Silvestri’s use of the combination in 1896. As the two species represented by the name *dorsalis* are now referred to quite different genera (neither of them *Platyrhacus*!) no problem with homonymy now exists.

***Acanthodesmus mortoni* (Carl)**

Figs 38-40

*Platyrrhacus mortoni* Carl, 1909: 255, figs 10, 11. Male holotype [MHNG] from “Borneo” without specific locality.

*Acanthodesmus mortoni*: Hoffman, 1984: 260, figs 2-4, 10, 11.

Remarks: The gonopod prefemur of the holotype presents a small but distinct acute projection in the same position (Fig. 38, arrow) as the much larger and longer process depicted by Attems for *A. anambasius*. Little would be required in the way of an annectant condition to bridge the existing difference, an additional justification for referring *anambasius* to this genus.

***Acanthodesmus picteti* (Silvestri)**

*Eurydirorhachis picteti* Silvestri, 1899: 332, pl. 15, figs 1, 2. Lectotype and paralectotypes [MHNG] from “Sarawak” without specific locality.

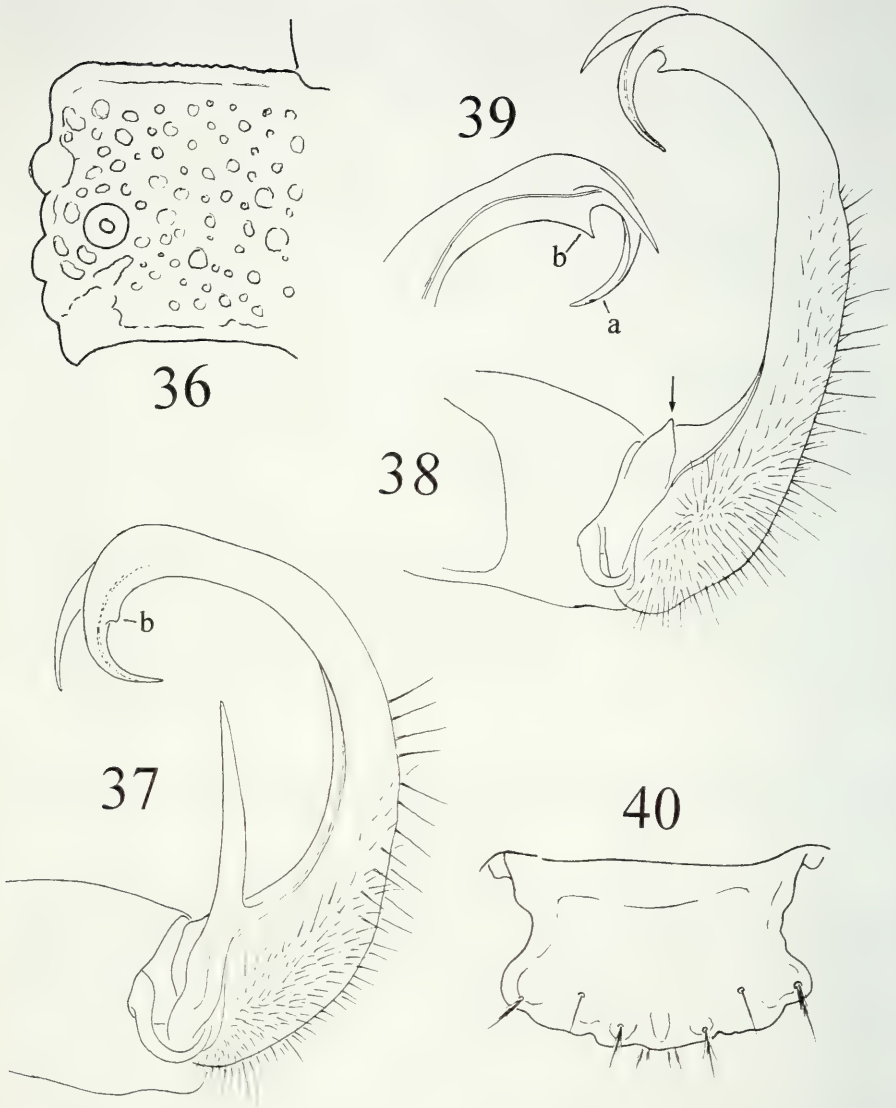
*Acanthodesmus picteti*: Hoffman, 1984: 260, figs 12, 13.

***Acanthodesmus pilipes* (Peters)**

Fig. 36

*Polydesmus (Acanthodesmus) pilipes* Peters, 1864: 544. Lectotype and paralectotype [ZMB] from “Pulo Matjan” [in error].

*Acanthodesmus pilipes*: Silvestri, 1896: 191.-- Hoffman, 1984: 261, figs 5-7, 14, 15.



Figs 36-40

*Acanthodesmus pilipes* (Peters), holotype (ZMP). Fig. 36. Left parantem of midbody segment.  
*Acanthodesmus anambasius* (Attems), holotype (ZMB). Fig. 37. Left gonopod, mesal aspect.  
*Acanthodesmus mortoni* (Carl), holotype (MHNG). Fig. 38. Left gonopod, mesal aspect; arrow indicates vestigial prefemoral process. Fig. 39. Distal half of telopodite of left gonopod, dorsal aspect. Fig. 40. Epiproct, dorsal aspect.



*Arbelorhacus* new genus

Type species: *A. magirus* sp. n.

Diagnosis: A genus of relatively small platyrrhacids, in which the gonotelopodite terminates in two processes only, a smaller, arcuately curved, subterminal solenomere (**a**) and a much larger and longer **d** which is laminately flattened, provided with a distinct subapical dentation, and is evenly curved more or less parallel to **a** (Figs 44 and 45).

Head granular, clypeal and labral compound setae set on enlarged, polished tubercles. Collum with distinct transverse ridge along median sector of anterior edge. Paranota of anterior segments gradually increasing in size posteriad, at midbody mostly transverse with anterior corner rounded, posterior rectangular, edges smooth back to posterior third, where anterior and posterior edges are notably denticulate; ozopores small, set about 3 diameters inward from lateral edge and near midlength of paranota. Surface of metaterga uniformly granular, without evident transverse rows of enlarged tubercles. Epiproct spatulate, constricted at base, distal edge slightly convex and shallowly crenulate. Legs attached to moderately elevated, narrow, unspined podosterna.

Name: A neologism composed of *arbelos* (Gk., a shoemaker's rounded knife) + *-rhacus*, a common element in this family, referring to the blade-like, apically hooked, process **D** of the gonopod. Gender masculine.

Remarks: This rather distinct genus, composed of species smaller than average for the Borneo fauna, includes also *Platyrrhacus baramanus* Attems, 1897. The two species are distinguished as follows:

KEY TO THE SPECIES OF *ARBELORHACUS*

- 1. Smaller species, ♂ 53 mm, width 8.0 mm; anterior edge of paranota of segments 12-17 with a row of 8-10 acute spicules; legs entirely yellow; transverse metatergal rows of tubercles scarcely visible . . . . . *magirus*
- Larger species, ♂ 63 mm, width 9.5 mm; anterior edge of paranota smooth; distal podomeres brown; transverse metatergal tubercle rows distinct . . . . . *baramanus*

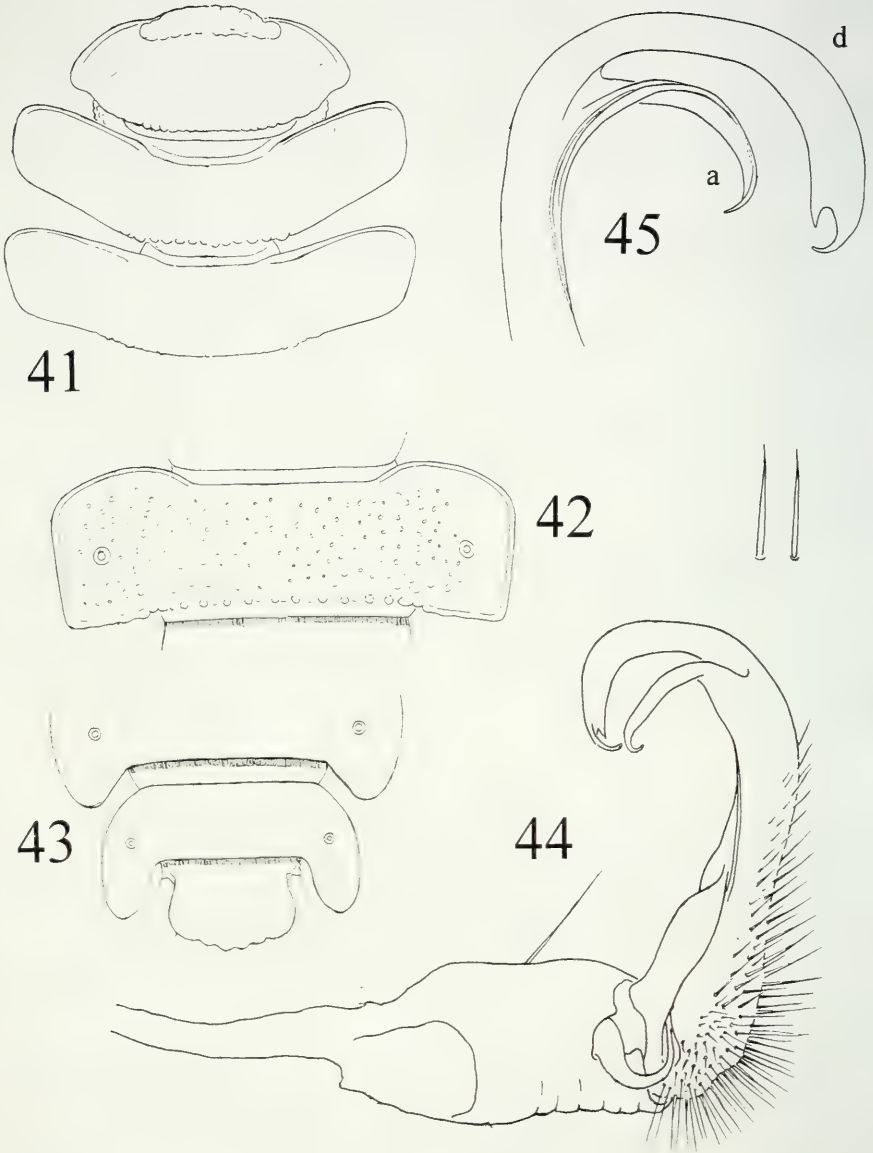
*Arbelorhacus magirus* sp. n. Figs 41-45

Material: Male holotype and three male paratypes [VMNH], male paratype [MHNG], from Mulu Caves National Park, **Sarawak**; J. M. Anderson leg. 2 September 1977.

Name: A Latinized form of the Greek word *mageiros* (a cook), commemorating the fundamental contributions of O. F. Cook to the classification of this family.

Holotype: Adult male, curled and broken, reconstructed length ca. 53 mm, widths of selected segments across paranota:

1 - 5.0 mm	10 - 8.0 mm
2 - 6.8	12 - 8.1
4 - 7.4	14 - 7.9
8 - 8.0	16 - 7.7



FIGS 41-45

*Arbelorhacus magirus*, sp. n., holotype (VMNH). Fig. 41. Collum and first two body segments. Fig. 42. midbody segment. Fig. 43. Epiproct and segments 18 and 19. Fig. 44. Left gonopod, mesal aspect, with two prefemoral setae (above) showing correct proportions. Fig. 45. Distal half of telopodite of left gonopod, dorsal aspect, enlarged.

Specimen discolored by preservation, but metaterga and posterior half of prozona brown, darker in and adjacent to stricture, entire dorsal surface of paranota, and most of epiproct, yellow; undersides and antennae nearly unpigmented, probably light yellowish-white in life.

Head granulate, clypeal setae 2-2, labral setae 3-3, lower genal setae 2-2, in all series borne on enlarged, polished tubercles; genae with distinct median depression, laterally an evident labroclypeal offset. Antennae relatively slender, articles at least twice as long as maximum width, none strongly clavate; interantennal isthmus about equal to length of basal antennomere.

Collum small, surface uniformly granular, a prominent elevated ridge formed from coalesced tubercles along median sector of anterior margin; shape of collum and next two metaterga as in Fig. 41. Paranota of midbody segments moderate in size, set high on body and nearly horizontal, of the shape shown in Fig. 42. Edges smooth back to about 13th segment, from whence both anterior and posterior edges are set with a single row of acute denticles. Ozopores small, remaining at about midlength of paranota on even posteriormost segments. Metatergal surface moderately and uniformly granulate, without transverse series of enlarged tubercles except traces of a row along posterior margin. Epiproct of the shape illustrated (Fig. 43), hypoproct of typical form, subtrapezoidal with enlarged paramedian distal tubercles. Legs set on elevated, narrow podosterna; no trace of subcoxal spines, intercoxal width about equal to length of a coxa. Legs long and slender, end of femora visible beyond paranota when extended laterad. Sides of metazona essentially smooth. Stigmata slightly auriculate with raised edges, posterior stigmata somewhat narrower as longer than anterior.

Gonopodal aperture small, rounded-oval, with lateral edges raised. Gonopods as described in generic diagnosis and illustrated in Figs 44 and 45. Coxae without enlarged or apically penicillate setae; coxae with distinctly thickened prefemoral setae (Fig. 44, above).

***Arbelorhacus baramanus*** (Attems) comb. n.

*Platyrrhacus baramanus* Attems, 1897: 495, fig. 15. Male and female syntypes [NMW] from the Baram River, 900-1000 m., Kalimantan, Indonesia, W. Kükenthal, leg.

*Platyrrhacus baramanus*: Attems, 1899: 331, fig. 320; Attems, 1914: 255; Attems, 1938: 218, fig. 237.

Description (abridged from Attems, 1897): Length 63-68 mm, width ♂ 9.5 mm, ♀ 11 mm. Prozona and anterior half of metaterga dark brown; posterior half of metaterga lighter brown. Paranota, venter, and basal podomeres yellow, distal podomeres brown.

Collum subellipsoid, anterior edge almost straight, slightly wider than the head, both anterior and posterior margins with a row of enlarged tubercles; disk with a transverse depression behind anterior margin.

Metaterga coarsely granulated, with three transverse rows of enlarged tubercles, those of the third row the largest; sides of metazona and entire prozona finely granulate. Dorsum somewhat convex, paranota nearly horizontal, broad, narrowly

marginated, the anteriormost directed anteriorly, from 15th segment becoming increasingly produced caudad; anterior and lateral edges smooth, posterior finely serrulate. Ozopores located near center of paranota, distant from lateral edge. Epiproct broad, lateral sides somewhat divergent caudad; posterior edge rounded, with 7-8 shallow indentations and large bristles. Hypoproct truncate, with a small median projection and two larger paramedian setiferous projections. Sterna densely setose, without spines.

Remarks: The elevation recorded for the type collection suggests a point near the headwaters of the Mahakkam River in the Müller Range, therefore about 360 km south of the type locality for *A. magirus*.

### ***Eurydirorhachis***

*Eurydirorhachis* Pocock, 1897: 435. Proposed with three new species. Type species: *E. dulitensis* Pocock, by subsequent designation of Hoffman, 1956.

*Eurydirorhachis*: Hoffman, 1984: 262.

Diagnosis: A genus of Bornean platyrhacids agreeing closely with *Acanthodesmus* in external structure, differing in (1) apical processes **a** and **b** present, slender, subequal, (2) no trace of process **c**, (2) telopodite much longer, acropodite region much longer than prefemoral and arcuately curved.

Remarks: Curiously, no specimens referable to this genus, aside the original types, have been found in the various collections available to me over the past several decades. No useful comments can thus be added to what I noted in 1984.

### ***Eurydirorhachis dulitensis*** Pocock

Fig. 46

*Eurydirorhachis dulitensis* Pocock, 1897: 436, fig. 10. Male holotype [BMNH] from "Mount Dulit, N. Borneo".

*Eurydirorhachis dulitensis*: Hoffman, 1984: 263, fig. 16.

### ***Eurydirorhachis plakodonota*** (Attems)

*Platyrhachus plakodonotus* Attems, 1897: 497, pl. 22, fig. 16. Syntypes [SMF] from "Borneo, Baramfluss."

*Eurydirorhachis plakodonotus*: Hoffman, 1984: 263.

As the publication date of Attems' description has still not been determined (and must be provisionally dated as 31 December 1897), it is unknown whether this name actually antedates the two published by Pocock in November of 1897.

### ***Eurydirorhachis baramanensis*** Pocock

*Eurydirorhachis baramanensis* Pocock, 1897: 436. Female holotype [BMNH] from "Baram, N. Borneo."



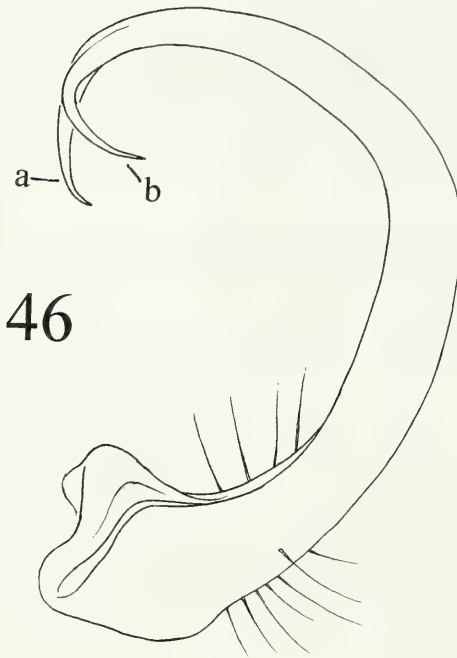


FIG. 46

*Eurydirorhachis dulitensis* Pocock, telopodite of left gonopod, holotype (BMNH).

### BIOGEOGRAPHIC INFERENCES

Inasmuch as all of the platyrhacid species (including those of immediately adjacent islands) recorded for the Borneo fauna are endemic, information about the geographic affinities of these millipeds must be sought at generic and tribal levels. Even here, owing to the absence of any comprehensive modern classification of the family, meaningful comparisons are difficult to derive.

Two of the tribal groups (Hoplurorhachini with the three genera *Hoplurorhachis*, *Creagrogonopus*, and *Sabarhacus*, and Phyodesmini with only one genus) appear to be endemic to the island, without even close relatives elsewhere (the case of the supposedly Sumatran species *gongylodes* is excluded, pending verification of the locality data by the collection of new material). In their peripheral structure and coloration, the species of *Phyodesmus* resemble Sumatran species like *princeps* (Gervais) and *mirandus* Pocock (neither yet assigned to the correct genus), but the gonopod structure is distinctly different.

In the tribe Platyrhacini, *Arbelorhacus*, *Acanthodesmus*, and *Eurydirorhachis* are endemic. Only *Stenoniodes* appears to have affinities with the large and multi-formous genus *Platyrhacus* which is widespread in Java, Sumatra, Malaysia, and "Indochina". In this case, whilst the gonopods are quite similar in the two nominal taxa, the form of the collum and paranota is strikingly different.

The absence of any members of the Papuan tribe Psaphodesmini from Borneo is notable. These millipeds appear to have been constrained by the factors contributing to "Wallace's Line". Equally interesting is the absence of any Bornean genera on the southern islands of the Philippines, as those known so far from Mindanao and Negros are endemics, of uncertain tribal assignation.

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